ANNALS
OF THE
ENTOMOLOGICAL SOCIETY OF AMERICA

Volume 52 May, 1959 Number 3

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the

ENTOMOLOGICAL SOCIETY OF AMERICA

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Second class postage paid at Columbus, Ohio. By order of Dec. 10, 1958.

Printed by The Spahr & Glenn Company,
50 East Broad Street
Columbus 15, Ohio, U. S. A.

Issued May 29, 1959

Annals of
The Entomological Society of America

Volume 52 MAY, 1959 No. 3

OBSERVATIONS ON LIVING HEMOCYTES IN WING VEINS OF THE COCKROACH BLABERUS GIGANTEUS (L.) (ORTHOPTERA: BLATTIDAE)[1]

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ABSTRACT

The hemocytes were observed daily in the wing veins during the insect's adult life. Blood circulation in the wing was vigorous and constant in young adults, but declined and was variable with increasing age. All of the veins gradually became occluded to some degree by hemocytes, but the main ones supported blood flow until the insect's death. With declining circulation in old adults, gas-hemocyte agglomerations developed around many tracheae, the hemocytes engulfing and surrounding gas bubbles that escaped from the tracheae. The hemocytes were divisible into two main classes, prohemocytes and plasmatocytes, which are described. The main class, plasmatocytes, were flexible and distinctive when young but became lax and variable in form and structure with increasing age, and according to the cell's history. This resulted in an apparently diverse cell complex.

Blood circulation in the wings of insects provides a means for observing clearly the living hemocytes in some species. Nevertheless, hemocytes have been described principally from fixed and stained blood films and insect sections. In vitro preparations of various kinds have been used by several authors and some observations of the cells in vivo in transparent larvae have been reported recently by Jones (1953) and Rizki (1953).

In view of the many discrepancies in the descriptions of hemocytes, some of which result from faulty preparation techniques or from use of different techniques by different authors, a knowledge of the in vivo characteristics of the cells is of particular importance. At least, it assists in interpreting the cell complex obtained by other means. At best, it may contribute to an understanding of the cell functions.

This is a report on the general nature of the hemocytes of *Blaberus giganteus* (L.) as observed in vivo in the wing veins. This knowledge was considered prerequisite to attempts to define the cell classes and determine their functions in this or similar species and in others where the hemocyte complex is obviously more diversified. General observations on circulation of blood in the wings are reported also.

[1]Contribution No. 3815, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada. Accepted for publication July 17, 1958.
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METHODS

Newly emerged male adults of *B. giganteus* were obtained periodically from the Pesticide Testing Laboratory, Canada Department of Agriculture, Ottawa. They were supplied with dog biscuits and water and held at 27° C. and 70 percent relative humidity. Three roaches were usually caged together and observations were made on the circulation of blood in the wings of a different individual each day until they died. This amount of handling probably contributed to an observed reduction in the adult life span but had no distinctive deleterious effects.

Blood circulation in the wings was observed in the following manner. The roach was lightly anesthetized with carbon dioxide and placed on its back on a specially devised aluminum slide (fig. 1), where it was held, without appreciable pressure, by elastic bands that were stretched across its legs and body from upright projections of the slide. Both wings of one side were positioned over a circular aperture in the slide for viewing with the compound microscope. With dry microscope objectives, the wings were immersed in water between thin glass coverslips. With the oil-immersion objective, the oil was placed directly on the wing surfaces. Observations were made principally with brightfield and on occasion with phase-contrast and darkfield illumination.

Negative photographs of wing venation (fig. 2)

were prepared by injecting a saline solution of neutral red into the wings of a newly killed roach and projecting them directly on enlarging paper.

Photomicrographs of the living, moving hemocytes were made with an electronic flash unit adapted for use with the Leitz Ortholux microscope. Several different units were used at different times, but most of the present photographs were made with a Braun Hobby Light (Braun Kundendienst, Frankfurt-am-Main, Germany). The flash reflector was removed and the naked, U-shaped flash tube centered in front

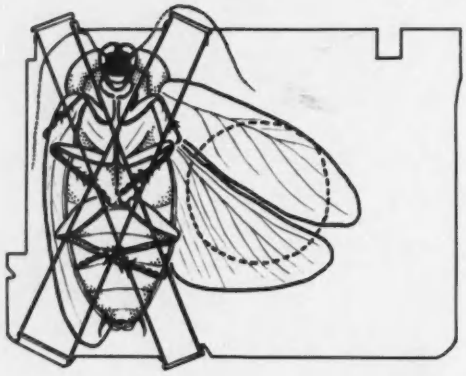


FIG. 1.—Slide for holding roach during observation of wing circulation.

of the microscope lamp house. In this way the hemocytes were observed with normal microscope illumination and photographed with light from the flash tube plus that of the microscope lamp. The camera used was a Kine-Exakta II (Ihagee, Dresden A 16, Germany). Bright-field illumination in conjunction with a Wratten B filter No. 58 (green) gave the most satisfactory photomicrographs and was used almost exclusively.

RESULTS AND DISCUSSION

Blood Ciruclation in the Wings.—The blood circulation in the wings (fig. 2) was generally similar to that in other cockroaches (Roeder 1953). The blood flowed outward from the body through approximately the anterior half of each wing and returned through the posterior half. It was confined in a complex system of vessels that also largely encompassed the tracheae and nerves of the wing. In addition to the obvious large vessels, a myriad of small veins formed a meshlike system by which the blood percolated through the wing. No blood sinuses occurred but in certain areas, particularly in the proximal region of the tegmina, the vessels were short, relatively wide, and very numerous, or were merely pathways among pillars of cuticle. Here the wing was almost completely bathed in blood.

The blood flow was vigorous and fairly constant in young adults but declined and was more variable with increasing age. It followed rather well-defined routes through the wing but meandered in the minor veins. It commonly moved in opposite directions in different portions of a given vein, and often in the same portion where a large, centrally located trachea bisected the lumen. The rate of flow fluctuated moderately when the insect was at rest but much more widely when it struggled. Thus on occasion the flow might falter, reverse momentarily, stop completely for brief intervals, or proceed in gushes. Similar but more moderate fluctuations sometimes occurred in old adults that were apparently quiet. The flow was retarded or stopped during the brief period of carbon dioxide anesthesia at the start of each observation. However, recovery was rapid and, unlike some other anesthetics, carbon dioxide had no visible effect on the hemocytes. Although spreading the wings is reported to interfere with circulation of blood in the wings (*Periplaneta americana* (L.), in Yeager and Henderickson 1934), it did not do so in *B. giganteus* with the angle of spread used.

The hemocytes were not uniformly distributed in the blood. In a given vein there was a moderate fluctuation in the number of cells passing a point in a unit of time, and there was considerable variation in the numbers passing through different veins, even those of similar size. Small veins not in the direct route of circulation, e. g., at right angles to the general direction of flow, often carried relatively few cells and at a slow rate. These veins often became occluded with hemocytes and the hemolymph gradually ceased to flow through them. In some cases, particularly where the occlusion developed after several weeks of adult life, the vein remained plugged with cells until the insect's death. In other instances, more often in young adults, the hemocytes forming the occlusion evidently degenerated as the vein was slowly obliterated by secretion of cuticle (fig. 3). Although the obliteration of a single vein was not followed, veins showing various degrees of stricture were fairly common in the distal areas of the wing. Generally, obliteration appeared to result from secretion of cuticle and started at the original site of occlusion and progressed outwards in both directions. It was not clear whether the hemocytes were involved in the secretion, or whether hypodermal cells remained in the vein and were responsible.

Although most of the veins became partly occluded by hemocytes as the insect grew older, the major channels supported a gradually declining circulation until the insect's death. Toward the end of adult life, sheets of gas bubbles appeared in many of the veins where tracheae occurred (fig. 4). Although a similar situation has been described for wings without circulation

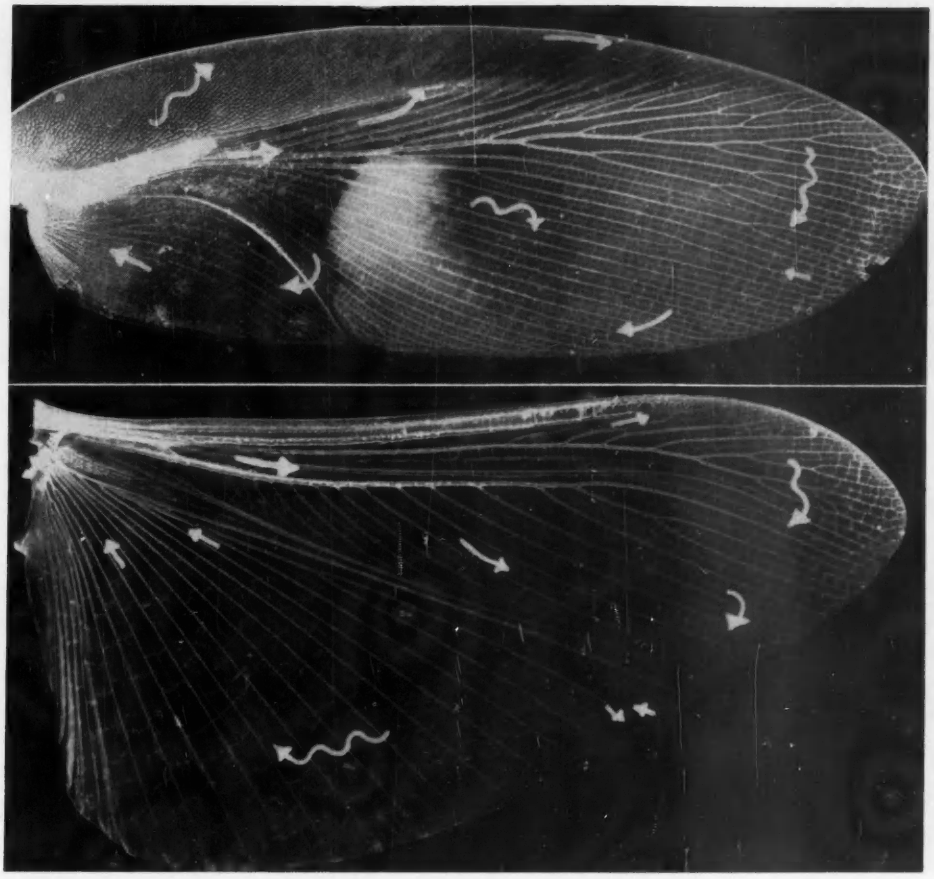


FIG. 2.—Wing venation. Arrows mark route of circulation. Approx. ×2.5.

(Tauber and Clare 1942), in *B. giganteus* it was a common feature of aging associated with declining circulation but not necessarily with its absence. The sheets had little obvious cellular structure but evidently comprised films of hemocytes among and within which gas bubbles, presumably from collapsing tracheae, were entrapped. This relationship of the hemocytes to the gas bubbles was demonstrated best in the formative stage of a sheet (fig. 5), after which the cellular details were almost completely lost. Apparently the cells engulfed small bubbles (fig. 6) and also spread over the surfaces of bubbles, preventing their coalescence. The sheets were usually attached to the vein walls by cellular extensions (fig. 7) and waved in the blood current. Occasionally portions of a sheet broke free in a surge of blood and were carried away. Infrequently single bubbles with one or more attached hemocytes or small groups of enmeshed bubbles (fig. 8) were seen flowing through a vein.

The tracheae, portions of which appear in several of the illustrations, were a common feature in the wings of this species and their role warrants consideration. Although it is generally considered that the blood has a very minor respiratory function in most insects (Roeder 1953), the presence of an extensive tracheal system in the wing veins and particularly the frequent knots of tracheoles suspended in the blood (fig. 9) indicate at least some gaseous exchange.

The Hemocytes in vivo.—The hemocyte complex in *B. giganteus* generally resembles that of other Orthoptera. Although a number of apparently different cell types occur in the circulating blood, they seem to be examples of hemocyte variation and not functionally or developmentally distinct forms. They can be accounted for, at least in part, by observable in vivo cell changes involving principally size, form, and the nature of the cytoplasm that are related fundamentally to the

age of the insect and/or the cell and to the cell's immediate or prior position. This is discussed more fully later. No attempt was made to distinguish functional cell types experimentally, but two classes were recognized.

The great majority of the circulating hemocytes were large, flat cells, usually 25 to 35 microns in greatest diameter, in which the nucleus occupied approximately one-third of the total cell area. They are here termed *plasmatocytes*, the name applied to typical phagocytes by Yeager (1945). In young adults about 60 percent of them were more or less fusiform and generally twisted slightly (fig. 10), like those of *P. americana* (Smith 1938). Most of the remainder were disc-shaped and a few were roughly spherical or polymorphic. The cell surface was relatively smooth and the edges rounded. With phase-contrast illumination the cytoplasm had a fine granular appearance, which is somewhat exaggerated in the bright-field photomicrographs. The plasmatocytes were very flexible and, although constantly squeezed and bent by the force of the blood current as they passed obstructions, they resumed their original shape immediately. They seldom clumped together at this time even though they were frequently piled up at obstacles for short periods.

A few of the cells were *prohemocytes*, characterized by their small size (about 10 microns in diameter) and small amount of cytoplasm (fig. 11). Their nuclear area typically exceeded or was equal to that of the cytoplasm. They were usually spherical and, possibly for this reason, less freely suspended in the hemolymph than the plasmatocytes. They apparently developed directly into plasmatocytes, and transitional stages were common. Dividing cells occurred rarely in adult blood, but films of nymphal blood showed mitotically dividing prohemocytes and plasmatocytes. The mitotic index was not determined.

As the insect became older the hemocyte complex underwent a number of changes. Prohemocytes occurred less frequently, except for the occasional resurgence in some old specimens, and the characteristics of the plasmatocytes altered greatly. The number of distinctly fusiform plasmatocytes declined and there was an accompanying increase in disc-shaped and polymorphic cells. The granulation of the cytoplasm was noticeably coarser, inclusions more numerous, and vacuolation more pronounced. The cell surface appeared rougher and more fragile, and the edges thin. Certain of these features are illustrated (figs. 12 and 13). There was also an increasing tendency for the cells to cling to obstacles, clump together, and attach themselves to the vein walls. The clumps often formed where a trachea obstructed a vein (fig. 14) or at vein junctions where eddies caused the cells to touch each other. Initially the cells appeared to be held by surface adhesion, but they slowly changed form and fitted together in a tissuelike clot (fig. 15). On the vein walls individual cells often attached at one edge or at one end so that the free portion undulated in the blood current or they settled flat on the surface of the vein. In the former case the cells sometimes remained for only a short period and at other times remained fixed and became a source of clotting. Where they were flat on the vein wall, the cells were of various forms but usually disc-shaped and frequently laden with globules (fig. 16). Blood films prepared at this time and stained with Giemsa blood stain showed that the globules were eosinophilic and that various numbers of them occurred in many of the hemocytes. Although the cytoplasm in some was filled with the globules, the cells were obviously plasmatocytes. The origin, constitution and significance of the globules were not determined. Eventually the vein walls accumulated several layers of hemocytes in some areas (fig. 17).

Extreme variations in hemocyte form and the various stages of cell degeneration were most common in old adults approaching death. Small numbers of young cells still occurred, but the majority appeared lax, were contorted into unusual shapes (figs. 18 and 19), and readily conformed to the outlines of the spaces into which they were moved by the current. Cytoplasmic protrusions, often threadlike, developed and contributed to vein occlusion. The final stages of cell degeneration were most evident in occluded veins and involved increasing cytoplasmic vacuolation, nuclear fragmentation, cell rupture and

EXPLANATION OF PLATE 1

FIG. 3.—Occluded wing vein showing degenerating hemocytes and stricture of vein by cuticle. Photo in sections. Approx. ×200.

FIG. 4.—Gas-hemocyte agglomerations around tracheae in wing veins of an old adult. Approx. ×200.

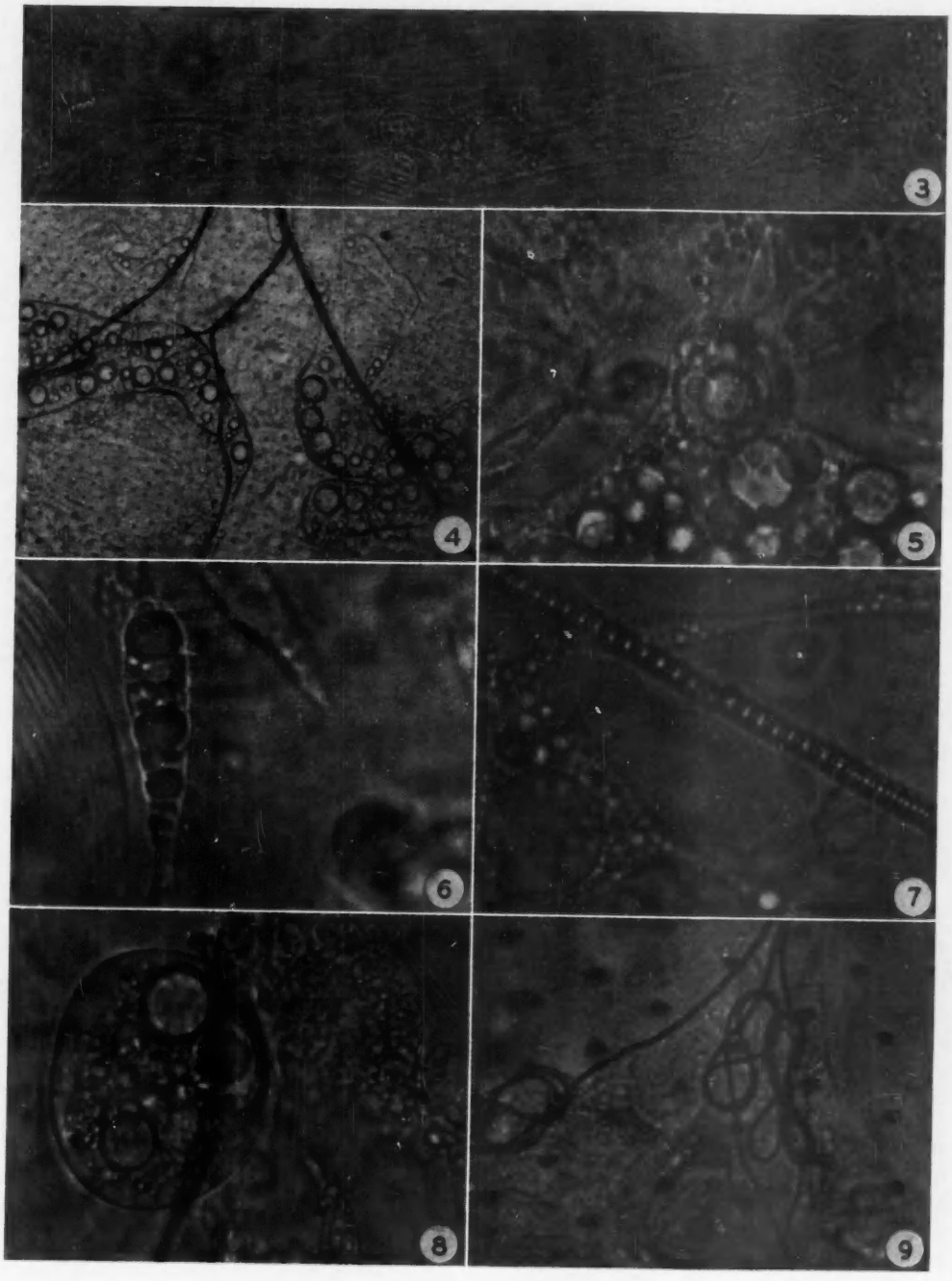
FIG. 5.—Forming gas-hemocyte agglomeration (below) with attached hemocytes extending across the lumen of the vein. Approx. ×700.

FIG. 6.—Hemocyte (left, attached to vein wall) with engulfed gas bubbles. Lumen of vein at right with free, moving hemocytes. Approx. ×900.

FIG. 7.—Gas-hemocyte agglomeration (left) showing filiform extensions to vein wall. Approx. ×700.

FIG. 8.—Small gas-hemocyte agglomeration moving in vein. Free hemocyte at bottom, right. Approx. ×700.

FIG. 9.—Tracheole knots in occluded wing vein of old adult. Approx. ×700.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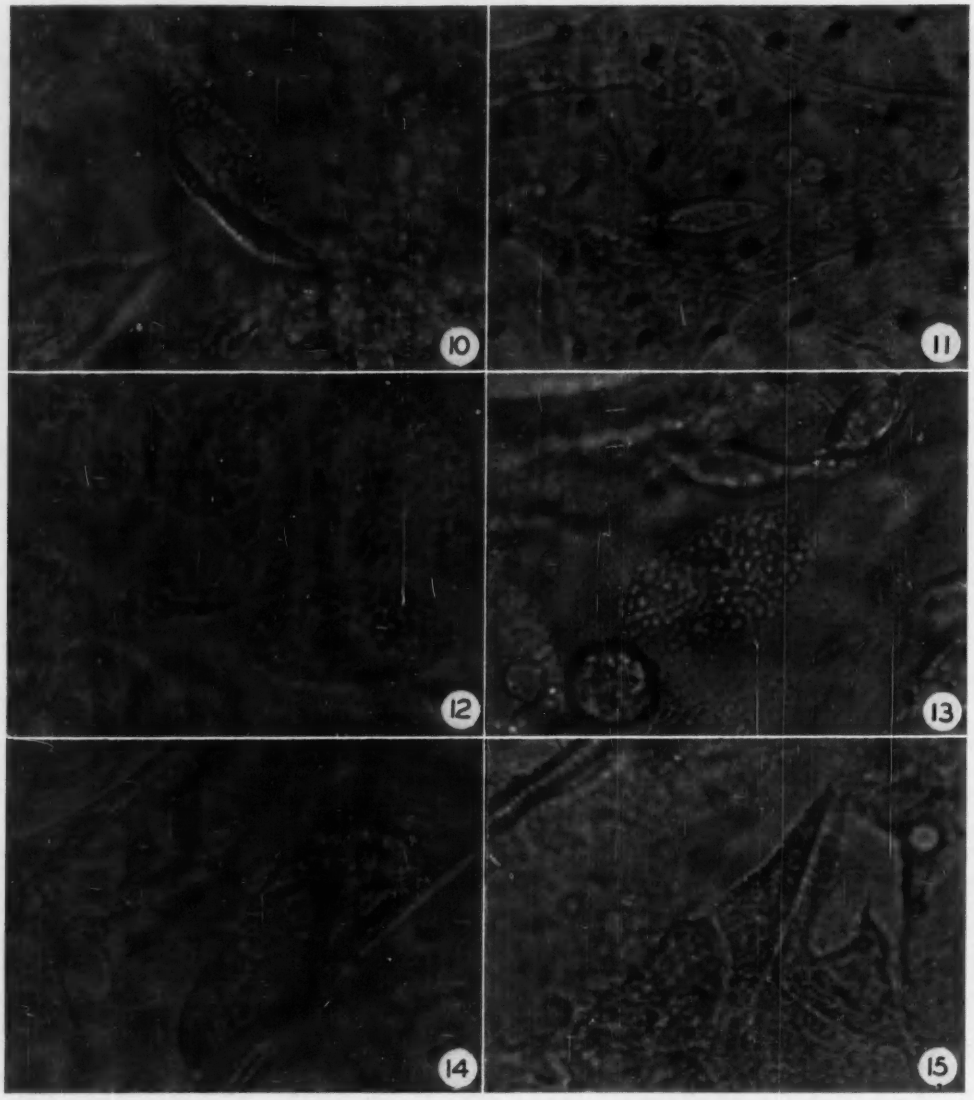

FIG. 10.—Typical fusiform plasmatocyte moving in vein. Approx. ×2000.

FIG. 11.—Two prohemocytes (in contact) and plasmatocyte in partly occluded vein of old adult. Approx. ×200.

FIG. 12.—Group of plasmatocytes, fusiform and disc-shaped, moving slowly in wing vein of old adult. Note heavy granulation. Approx. ×2000.

FIG. 13.—Plasmatocyte in early stage of degeneration moving in wing vein. Note vacuolation and scalloped surface. Approx. ×2000.

FIG. 14.—Clump of hemocytes forming at trachea (right). Fusiform and disc-shaped plasmatocytes flowing past clump. Approx. ×700.

FIG. 15.—Edge of hemocyte clump showing change of cell form. Approx. ×2000.

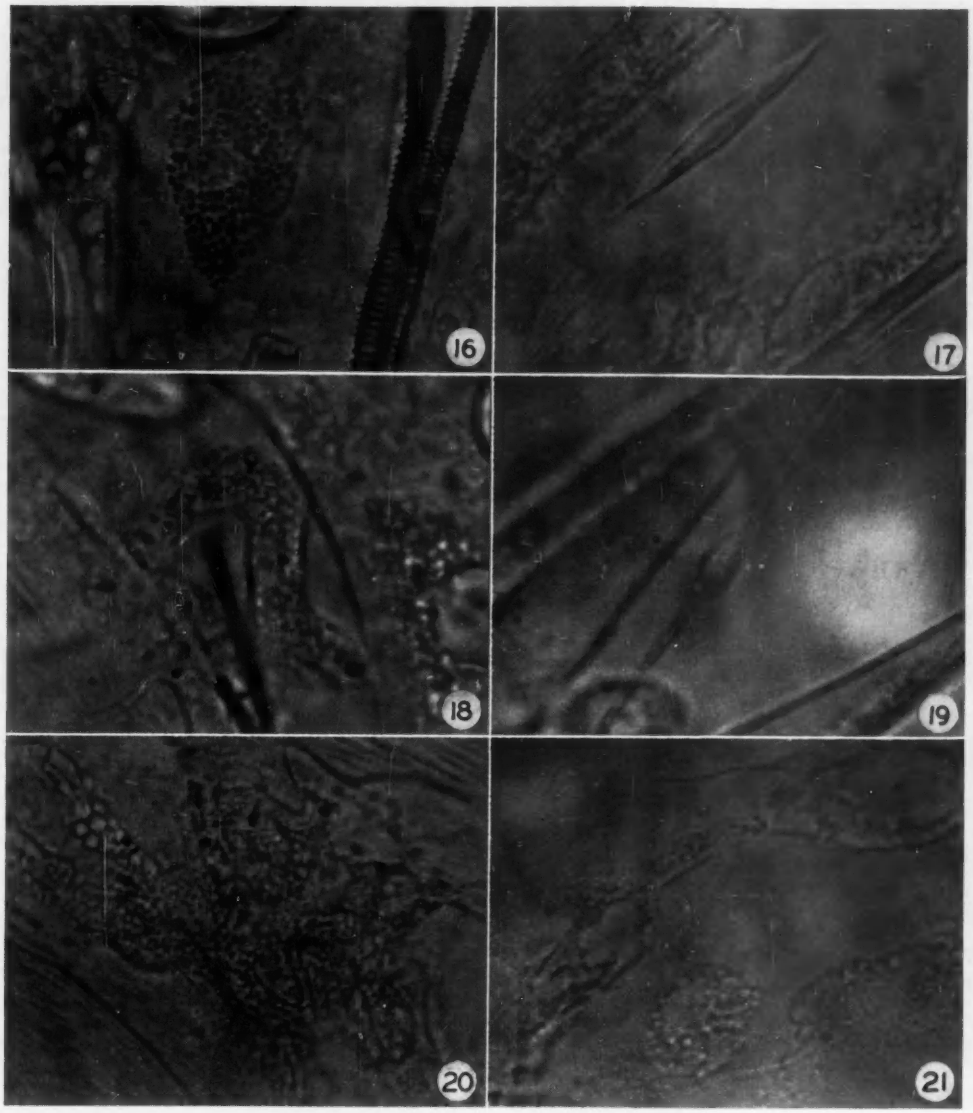

FIG. 16.—Plasmatocyte with globules in cytoplasm lying flat on vein wall. Approx. ×2000.

FIG. 17.—Edge view of fast-moving plasmatocyte in center of vein. Note layer of hemocytes on vein wall. Approx. ×2000.

FIG. 18.—Old plasmatocyte contorted into unusual shape moving slowly in partly occluded vein. Approx. ×2000.

FIG. 19.—Extremely elongate plasmatocyte extending across a vein in old adult. Approx. ×2000.

FIG. 20.—Vein occluded with degenerating hemocytes. Note cellular extensions and vacuolation. Approx. ×900.

FIG. 21.—Previously occluded vein reopened after degeneration of hemocytes. Note hemocyte remnants on walls and disc-shaped plasmatocyte moving through. Approx. ×900.

dispersal (fig. 20). In a few instances veins were observed to reopen (fig. 21) after degeneration of the hemocyte mass.

Some of the hemocyte variations were obviously related to the age of the insect and/or the cell as shown by the changing cell complex. Some derived also from the cell's situation, for example, whether the cell was suspended freely in the circulating blood, resting on a vein wall, lodged in a vein where the flow of hemolymph was poor, or entangled in a loose clump of hemocytes. Frequently, cells that were lodged in a vein under specific circumstances were observed continuously for periods up to 2 hours, during which some changes usually occurred, and other cells in similar circumstances were noted on succeeding days. An outstanding feature of the observed changes, which inevitably involved aging, was that they developed slowly. Even the alteration of cell form, which might be presumed to occur rapidly and does so under abnormal conditions in at least one species (Arnold 1952), was often apparent only after the cell had remained 30 minutes or more in one situation. Frequently, after undergoing a change, cells were swept back into circulation; presumably this occurs continually throughout the insect's body. Consequently, the circulating blood contained hemocytes of various ages and with diverse characteristics that also reflected their temporary exposure to different situations. Presumably some situations that the cells meet in the body, such as adherence to various kinds of tissues, influence their nature considerably.

In view of these observations it seems logical to use only the simplest classification for the hemocytes unless experimental studies demonstrate fundamental distinctions among them. Furthermore, interpretation of the hemocyte complex from prepared blood films alone, which has been the common practice, or from any single technique including the one employed here, seems unwise. Several techniques should be used and attention should be given to the age of the insect and the source of the blood in addition to the generally accepted factors of species and methods of fixation and staining. Although an in vivo method was used principally in this study, reference to in vitro preparations and stained films was necessary on occasion. Undoubtedly the in vivo method would be unsatisfactory for many species, but it served in this case to demonstrate certain characteristics of the hemocytes and should prove useful in future experimental studies.

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LOCALIZING EFFECTS OF HUMAN HOSTS ON THE MOSQUITO MANSONIA PERTURBANS[1]

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ABSTRACT

Field tests to determine the localizing effect of man on the mosquito, *Mansonia perturbans* (Walker), were made by use of a human subject beneath a drop net and in a parked car along a swamp margin during the early evening activity period. Records from seven tests in June 1958 showed that sizable groups of mosquitoes were localized in resting position when man was present. Male swarms were also deactivated beneath the drop net and in the parked car with the host.

Observations by Snow and Pickard (1958) on the prevalence of *M. perturbans* during the evening peak period at Beaverdam Swamp, Greenbrier, Alabama, in June and July 1957 revealed that a sizable number of mosquitoes came to rest in the vicinity of man without biting. This was particularly evident where immediate artificial resting surfaces were present such as the frame and folded net of a drop-net device and the interior of a parked car. One test also revealed that when

[1]Accepted for publication October 9, 1958.

FIG. 1.—Position of the mosquito collecting stations used in evaluating the localizing effects of man on *Mansonia perturbans*, Beaverdam Swamp, Greenbrier, Alabama, June 1958.

the period of observation was extended from 15 to 45 minutes after the 0.9 foot-candle level had been reached, the attacking and resting portions of the mosquito population had become more or less stabilized. Tests in the early summer of 1958 at the same location were designed to measure the localizing effect of the host where a confinable resting surface was afforded the mosquitoes. In five tests an open parked car with host and an open parked car without host (control) were used. In two tests human hosts were present in both cars. Simultaneous collections were also made by a man beneath the drop net and by a man in the open in order to provide additional comparisons on the localizing effects and the disposition of mosquitoes towards entering and feeding or resting under covered situations.

Although the 1958 series of tests were carried out in the same relative position along the south margin of the swamp as the 1957 tests, the background conditions were quite different. Vegetational cover in 1957 was generally dark and consisted mainly of composite and blackberry cover volunteering at the edge of the pasture. In 1958 the area was disked and seeded to rye grass. Hence, the black cars were considerably more prominent on a landscape composed of straw-colored grass (fig. 1). The collecting stations were situated in a west-east sequence such that the drop-net device and collector, exposed collector, parked car A, and parked car B were separated by about 50-foot intervals. In the series of five tests the human host occupied the parked car in A position and no host was used in the parked car in B position. In two tests human hosts were employed in each of the cars in A and B positions. The cars were alternated to minimize any selectivity. As in the 1957 tests the drop net was released and the car doors closed at the end of the test period to determine the numbers and species composition of the resting mosquito population.

Collections were initiated when pronounced feeding began in the dusk period and terminated after a 45-minute exposure period. In the first two tests on June 3 and 5 light intensity was 4.0 and 2.5 ft.-c., respectively, when pronounced feeding was experienced. In subsequent tests light

Table 1.—Captures of *Mansonia perturbans* on man and on artificial resting surfaces under protected and open conditions during the early evening activity period at Beaverdam Swamp, Greenbrier, Alabama, June 1958.

Date:	June										Total	
Weather:	3 Clear		5 Cloudy		10 Clear		17 Clear		18 Cloudy			
°F. Outside Car:	70–68		78–73		77–69.5		73.5–70.5		72–70			
°F. Inside Car:	76–73		79–79		80–76		74–74		79–76			
	M	F	M	F	M	F	M	F	M	F	M	F
Method												
1. Aspirating on man under drop net	2	365	5	477	0	480	0	380	0	278	7	1,908
Drop net catch	8	441	101	669	8	1081	1	84	0	325	118	2,600
2. Aspirating on man in open	0	490	0	532	0	700	0	166	0	553	0	2,441
3. Aspirating on man in parked car A	0	50	0	332	0	285	0	86	0	81	0	834
Resting residual in car A	4	661	108	913	8	2267	1	244	0	188	121	4,273
4. Resting residual in car B without man	1	2	0	3	0	8	0	2	0	0	1	15
Total	15	2009	214	2926	16	4821	2	890	0	1425	247	12,071

intensity had declined to the 1.0 ft.-c. level before heavy attack was noted. A Weston photometer, model 756, with a self-generating selenium photocell Luxtron No. 7-1A, was used for all foot-candle readings.

RESULTS AND DISCUSSION

Results of the five tests utilizing the drop net device and collector, exposed collector, and baited and unbaited cars simultaneously are given in table 1. Considering the 12,318 specimens of *M. perturbans* captured in these tests, 12,071 or 98 percent were females. Of these, 1,908 or 15.8 percent were collected on man beneath the drop net and 2,600 or 21.5 percent were included in the drop net catch at the end of the collection period. The exposed collector captured 2,441 female *M. perturbans* or 20.2 percent of the females recovered in the five tests. In parked car A, 834 mosquitoes or 6.9 percent were aspirated from the collector and 4,273 or 35.4 percent were found mainly in resting position within the car at the end of the period. Only 15 female *M. perturbans* or 0.1 percent of the total were recovered from the interior of unbaited car B at the end of the 45-minute exposure period. The 247 male mosquitoes were about evenly divided between the drop-net method (125) and parked car A with host (121).

Since flight and feeding activity of *M. perturbans* had practically ceased along the swamp margin 45 minutes after the 1.0 ft.-c. level had been reached, the drop net and parked car A residuals may be said to represent deactivated or resting populations. In the five tests reported in table 1 the number of *M. perturbans* taken on man under the net and those resting on the inner surfaces of the drop net device was fairly close, 1,908 to 2,600 or 42.3 percent to 57.6 percent, respectively. In the parked car with human host over five times as many female mosquitoes, 4,273 or 83.7 percent, came to rest on the interior as actually landed on and attacked the host, 834 or 16.3 percent.

The proportionate difference between numbers captured on the hosts and on the resting surfaces available under the drop net and in the parked car may be attributed partly to a delay in the mosquitoes' entry of the parked car and partly to conditions less favorable for capture in the car interior. However, the fact that most of the mosquitoes entering the car remained in resting position at the end of the 45-minute exposure period is good evidence that they were not greatly stimulated to attack or feed under the existing conditions.

The role which the human host plays in localizing mosquitoes on resting surfaces in his vicinity could not be properly evaluated for the single drop-net device available but was clearly demonstrated for the parked car technique as a control car was provided. In the case of the drop net an inference of the localizing effect by man can be obtained by noting the difference between those taken on man in the open (2,441) and those on man beneath the net (1,908) plus those resting on the inner surfaces of the net (2,600). The collectors were known to be of equal efficiency, and, barring a disproportionate attack which occurred on June 17, it is possible that many of the mosquitoes approaching the collector under the drop net either rested temporarily on the net before attack

or were momentarily discouraged by failure to find a suitable feeding surface and became deactivated prior to a subsequent try. At least the end result was that while fewer mosquitoes generally fed on man beneath the net than in the open, an even greater number were shown to be still immediately available for attack at the end of the period. It was also noted that many mosquitoes came to rest on the outer upper surfaces of the net during the period and this portion of the population was not counted. More mosquitoes were probably captured by the exposed collector because he was in a more prominent position on the landscape and void of superfluous landing surfaces.

In the case of the parked-car collections there was a very striking difference in the resting populations when a human host was present or absent. The record of five tests showed that 4,273 of the 5,107 mosquitoes entering the occupied car were disinclined to feed on man at the time but remained on the interior of the car. In the vacant car (control) a total of only 15 female *M. perturbans* was found at the end of the test period. On the night of June 10 a maximum of 2,552 females entered the occupied car while only 8 were recorded from the unoccupied car.

That the site or relative position of the vehicles might be responsible for high localizing in the occupied car and low residual in the unoccupied car was disproved in tests employing human hosts in both vehicles on June 12 and June 19. The results given in table 2 show that the car in the end position (car B) was quite capable of retaining *M. perturbans* when provided with a human host. On June 12, resting residuals in occupied cars A and B were 451 and 436 female *M. perturbans*, respectively, whereas on June 10 when car A was occupied and car B unoccupied the count was 2,267 and 8, respectively. Although overall densities were somewhat lower on June 19 in the evening period, still 198 female mosquitoes remained resting in car B with host, though combined collections from the car in B position without host on the two previous evenings (June 17 and 18) yielded only two specimens. Parked car A with host showed 105 mosquitoes in resting position at the termination of the period on June 19.

Although the sampling techniques used at Beaverdam Swamp in June 1958 did not include an adequate sampling method for the male population of *M. perturbans* as used in 1957, a comparatively high number of males were captured following swarming beneath the drop net and in the parked car on June 5. Both swarms contained slightly over a hundred males with 106 accounted for in the drop net method and 108 in the occupied car. Swarming was first noted when light intensity had declined to the 2.0 ft.-c. level and continued for several minutes thereafter at least below the 1.0 ft.-c. mark. The swarm associated with the drop-net device was oriented between the collector's head and the top of the net, mainly on the east side or away from the western sky where scant light still prevailed. One coupled pair settled on the collector's arm and then separated and flew off quickly. Swarming in the parked car occurred over the front seat to the right of the collector (seated at the steering wheel) at the same time as beneath the drop net. Swarming individuals were noted swirling about intermittently in both situations, but, since the principal objective of the test was to aspirate mosquitoes attacking the collectors, close observations on the behavior of the swarms were not possible. A slight southwesterly breeze (2 feet per second) was present at the time of swarming and the sky was overcast with occasional thunder to the southwest. Air temperature was 78° F. beneath the drop net and 79° F. in the parked car. The relative humidity was about 60 percent.

Table 2.—Captures of *Mansonia perturbans* on man and artificial resting surfaces under protected and open conditions during the early evening activity period, Beaverdam Swamp, Greenbrier, Alabama, June 1958.

Date:	June 12		June 19		Total	
Weather:	Cloudy		Cloudy			
Temp. Range, °F.:	80–76		72–71			
Temp. Range, Car A:	82–80		73–72.5			
Temp. Range, Car B:	83–80		73–73			
	M	F	M	F	M	F
Method						
1. Aspirating on man under drop-net	1	302	0	222	1	524
Drop-net catch	3	463	0	131	3	594
2. Aspirating on man in open	1	504	0	312	1	816
3. Aspirating on man in parked car A	0	171	0	89	0	260
Residual in car A	2	451	0	105	2	556
Aspirating on man in parked car B	0	153	0	228	0	381
Residual in car B	4	436	0	198	4	634
Total	11	2480	0	1285	11	3765

ACKNOWLEDGMENT

Grateful acknowledgment is made to Dr. G. E. Smith, Chief Biologist, Division of Health and Safety, Tennessee Valley Authority, for guidance with the field studies. Special thanks are due Mr. J. L. Hawkins and Mr. P. K. Anderson, Biology Section, for assistance with the field collections.

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THE VARIATION IN THE BLOOD-CELL COUNT OF PERIPLANETA AMERICANA (L.) DURING A MOLT[1]

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ABSTRACT

The total blood cell count of the American cockroach was examined by counting a large number of samples from individuals selected from a laboratory culture. The results indicate that the intraspecific variation is too great to establish a normal count which can be used as a basis for comparison to determine abnormalities caused by external factors. The data also show that there is a significant reduction in the blood cell population at the time of a molt which is followed by a very rapid recovery in cell numbers immediately after the skin is shed.

The blood-cell population of insects has been the object of a number of studies. It is an easy and obvious criterion for use in the evaluation of physiological disturbances. It is easily demonstrated that the blood-cell population of insects can be reduced or obliterated by injecting foreign bodies such as vertebrate erythrocytes (Bettini et al. 1951) or chemicals, particularly alcohols. The phagocytic action of the cells can be blocked to a lesser extent with carbon black, and Yeager et al. (1942) used this technique to study the function of blood cells in detoxication. The essentiality of the blood cells to the insect can be demonstrated by plotting survival data against the percent of the normal compliment that remains after treatment with a material which reduces the number. A mortality of 50 percent can be expected for the American cockroach if the count is reduced to 35 percent of the normal based on a before and after treatment count from the same individual. Death usually is associated with septicemic infection, but aseptic insects are not able to survive such a reduction in the cell population, so that infection is not the only factor.

In order to use the total blood-cell count for comparative work it is necessary to have a normal count which will serve as a basis of comparison. Tauber and Yeager (1934, 1935, 1936) and Tauber (1937) published data listing total counts of a number of species. Experience with total counts made on the blood of late-instar nymphs of the American cockroach led to the series of investigations to be described. In order to elucidate the variation which was apparent, blood samples were counted from approximately 1,000 late-instar nymphs. The analyzed data which are presented represent samples taken from this series known to be free of technical errors such as coagulation, dilution, etc.

METHODS

Counts were made using a standard hemocytometer counting plate. One microliter blood samples were drawn from a clipped antenna or from a coxal joint and diluted 100 times. A special pipette (figure 1) similar to a white blood-dilution pipette was used. It differed principally in the provision for precisely measuring one microliter and diluting it 100 times. Several diluting media were used with moderate success. Tuerk's solution, which is used for vertebrate white-blood-cell counting, was suggested by Yeager

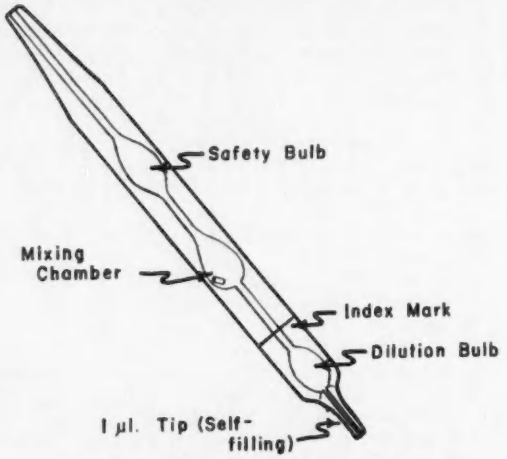

FIG. 1.—Blood dilution pipette.

(1935) and this was partially satisfactory, but did not stop blood coagulation in all samples. The same was experienced with oxalate. A better medium was a 1 to 2 percent solution of Versene (ethylene diaminetetraacetic acid tetrasodium salt—also known as sequestrene) as suggested by Grégoire (1951). This is a sequestering agent which chelates most metallic ions. No indication of its mode of action in this application is suggested. The pipettes with the diluted blood were shaken for several minutes on a mechanical shaker to disperse cells uniformly. The insects were selected from a laboratory colony and duplicate counts were made with each sample to check counting error. With some insects counts were made at either an hourly or daily interval during the molting period. The data obtained from

[1]Accepted for publication October 20, 1958.

these was fortified with counts made on insects selected from the colonies which were within 24 hours before a molt and those which had just emerged from their ecdysial skins. The premolt stage was determined by observing the eye color. Twenty-four hours before a molt the outer layers of the integument separate from the inner layers, which produces a distinct smoky-blue color to the eyes. This character is very useful in either selecting or avoiding the premolt stage.

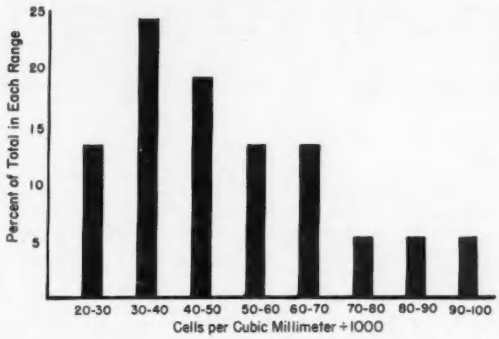

FIG. 2.—Distribution of total cell count from normal insects.

RESULTS

The results indicate that the blood-cell count of insects varies significantly intraspecifically and with the stage of development. From counts on 160 insects known to be between molts the mean total count was 50,400 cells per cubic millimeter. The standard deviation was 21,000 and the total range between 21,000 and 99,000 cells per cubic millimeter. The median count is between 30,000 and 40,000 cells per cubic millimeter. This is in reasonable agreement with the published values (Tauber and Yeager 1935). The distribution of the count in the sample is shown in figure 2. From these data it is apparent that a norm must be established for each individual before the total blood-cell count can be used as a satisfactory criterion of any physiological disturbance. Successive counts from the same insect are possible and reasonable agreement (within the 10 percent counting error) should be expected. Successive samples should be drawn from different sites on the animal. If this precaution is not observed it will result in an exaggerated count, clumping of cells, abnormal cells, and an accumulation of bacteria.

While making routine counts it was observed that the total blood-cell number is significantly diminished at the time of a molt. This is contrary to previously recorded data (Tauber and Yeager 1935) and was subjected to further study. Insects were selected on the basis of their eye color, and successive counts were made starting with the premolt stage at hourly intervals with a few insects and at 24-hour intervals with many. The handling and treatment at this stage proved to be very injurious and the mortality was high, particularly when hourly samples were taken. The results of the hourly counts which were completed support the general contour of the curve which resulted from data taken from the 24-hour series. The change in the total count during the molting period is shown in figure 3. There is a very sharp reduction in the numbers of blood cells, with a minimum at or near the time of emergence from the old skin. The onset of the decrease is about 48 hours before the molt, and becomes very apparent at the 24-hour period. Median values are plotted in figure 3. The range at 24 hours before the molt was between 20,000 and 46,000 cells per cubic millimeter. At the time of emergence the range was between 3,000 and 10,000, and 24 hours later the range was between 33,000 and 57,000 cells per cubic millimeter. The trend as expressed on the curve indicates as great as a ten-fold diminution of the cell count followed by a rapid recovery. During the period of minimum count the blood plasma is filled with bacteria and cell detritus. This condition normally clears completely when

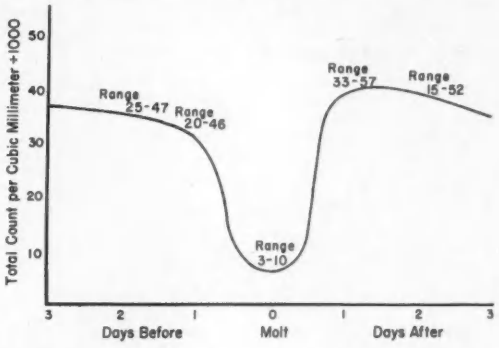

FIG. 3.—Total count at 24-hour intervals during a molt.

the cell population returns to normal. Photomicrographs of blood samples from the same insect taken 24 hours before the molt, during the molting process, and 2 weeks after the molt are shown in figures 4, 5, and 6.

DISCUSSION

This study was initiated to establish a normal blood count which could be used for comparison in experimental work. The results indicate that this is not reasonable, that individual determinations must be made for comparative work, and that the imminence of a molt is a significant factor in the application of this criterion.

The reduction in the count at the time of a molt with the very rapid buildup within 24 hours

FIG. 4.—Blood cell picture 24 hours before molt.

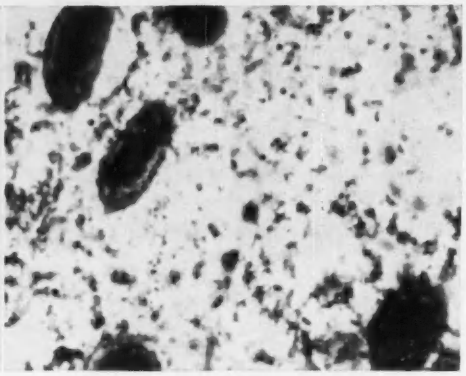

FIG. 5.—Blood cell picture during molt.

following is interpreted to indicate the presence of an hematopoetic tissue.

Microscopic examination of the blood cells divulged three types. These include plasmatocytes, which are predominant under normal conditions between molts; the proleukocytes, which may be juveniles, are abundant immediately following a molt; and an injured type of cell characterized by a bar-shaped nucleus. This type of cell is predominant when successive samples are taken from the same site on the insect.

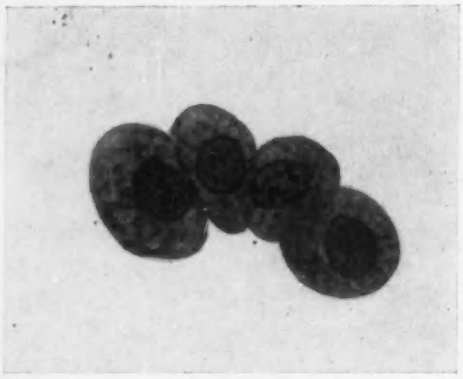

FIG. 6.—Blood cell picture 2 weeks after molt.

SUMMARY

These data were accumulated to describe the normal blood-cell count of an insect for the purposes of comparison in experimental work. The results show that large variations exist both in random samples of a colony of normal insects and with the imminence of a molt. Cognizance of these changes is important where total cell count is a criterion of the effect of an experimental factor.

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OBSERVATIONS ON EGYPTIAN HYALOMMA TICKS (IXODOIDEA, IXODIDAE). 5. BIOLOGICAL NOTES AND DIFFERENCES IN IDENTITY OF H. ANATOLICUM AND ITS SUBSPECIES ANATOLICUM KOCH AND EXCAVATUM KOCH AMONG RUSSIAN AND OTHER WORKERS. IDENTITY OF H. LUSITANICUM KOCH[1]

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ABSTRACT

Exhaustive study of very considerable material confirms the opinions of the Pomerantzev school that (1) *Hyalomma anatolicum* Koch and *H. excavatum* Koch are taxonomically valid subspecies (of *anatolicum*), (2) the subspecies *anatolicum* is that which non-Soviet workers have been referring to as *H. excavatum*, sensu Delpy, and (3) the subspecies *excavatum* is that which non-Soviet workers have been calling *anatolicum*, sensu Delpy. The immature stages of the subspecies *excavatum*, which differ morphologically from those of *anatolicum*, feed on rodents, rabbits and hares, whereas those of *anatolicum* generally feed on larger domestic animals. The former subspecies breeds actively during the winter months (in North Africa, at least), while the latter usually undergoes a winter dispause. These forms, which rank high among the world's economically most important ticks, range from southern Europe and northern Africa through the Near and Middle East to the Indian sub-continent. Narrowly elongate samples from populations at the eastern end of this range suggest the presence of yet another subspecies in this area (rearing experiments to determine their status presently underway will require a year or more for completion). *H. a. anatolicum* is usually more numerous than *H. a. excavatum* and is more uniformly distributed, while *excavatum* is absent in certain ecological zones where *anatolicum* is present. Intergradation is nil in most areas, but ranges from 2 to less than 20 percent among certain Mediterranean littoral populations of Egypt and Libya. Movements of domestic animals appear in some areas to break down partially the ecological isolation of the two forms. The subgenus *Hyalommina* Schulze, 1919, and the species *H. rhipicephaloides* Neumann, 1901, are regarded as synonyms of *Hyalomma* and of *H. anatolicum*, respectively; subgenus *Delpyiella* Santos Dias, 1956, erected for the Indian *H. hussaini* Sharif, is found to be valid. *Hyalomma lusitanicum* Koch, 1844, synonymized with *H. anatolicum* by many workers, is found to be a valid species occurring in southwestern Europe, the Canary Islands, and Morocco. Morphological and biological characters of the recently recognized *H. franchinii* Tonelli-Rondelli, 1932, are compared with those of the *anatolicum* complex, for which keys to males and females are provided.

The present report presents findings resulting from taxonomic and biologic studies of the form referred to as *Hyalomma* species number 2 near *excavatum* by Hoogstraal (1956). Review of Soviet literature and comparative study of specimens in the Schulze and in several other collections, including some sent to us by Russian workers, reveal that the names *H. anatolicum* (or *H. a. anatolicum*) and *H. excavatum* (or *H. anatolicum excavatum*) have long been used in exactly the reverse sense by Russian and non-Russian students. A vast amount of medical and veterinary literature deals with the two subspecies in the U.S.S.R. and elsewhere; these concern Uzbekistan hemorrhagic fever, various other encephalitic viruses, Q fever, theileriasis, piroplasmosis, etc. It is, therefore, especially desirable to be certain of the application of specific and subspecific names of the ticks involved as reservoirs or vectors in Europe, Africa, and Asia.

From Kratz's (1940) and Feldman-Muhsam's (1954) descriptions, measurements, and illustrations of the type specimen of *H. excavatum* Koch, it is evident that the Pomerantzev school has been correct in referring to the larger-size, less common subspecies of *H. anatolicum* as *excavatum* (sensu Pomerantzev, not Delpy). The smaller-size, more common subspecies, *excavatum* of Delpy, Feldman-Muhsam, and the writers therefore now becomes *H. a. anatolicum* (sensu Pomerantzev, not Schulze). Although this reversal undoubtedly will cause some temporary taxonomic turmoil, it does not affect the bulk of significant literature references to these two forms, which are largely in Russian publications owing to these ticks' ubiquity and economic importance there.

Unless otherwise indicated, the names *anatolicum* and *excavatum* are used sensu Pomerantzev throughout the present paper.

The synoptic lists in the following text include only those names from more important generic reviews and others that we are now certain are synonymous. During the past decade the enormity of earlier indiscriminate naming of species, subspecies, and sub-subspecies in this genus has been equalled by similarly indiscriminate, whimsical lumping of names for biologically and morphologically distinct populations by reviewers who failed to obtain representative samples for comparative study.

All material noted herein was collected by one or both of the writers, presented by various

[1]Research Report NM 52 08 03.12. The opinions and assertions contained herein are the private ones of the authors and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large. Accepted for publication July 28, 1958.

colleagues (NAMRU–3), or studied by them for the Rocky Mountain Laboratory (RML), and the British Museum (Natural History) (BMNH).

Hyalomma (Hyalomma) anatolicum anatolicum Koch (= *H. excavatum* of Delpy and non-Soviet workers)

The Small Hyalomma

(Figures 1–12, 27)

Hyalomma anatolicum Koch, 1844, pp. 220–221; short description of ♀ only; type locality "Kleinasien" (i.e., eastern Turkey).

H. anatolicum Koch; Koch, 1847, pp. 13, 35–36, Plate 3, Fig. 9, ♀ redescribed and illustrated.

H. rhipicephaloides Neumann, 1901. A considerable amount of evidence indicates that representatives of this "species" are no more than abnormal specimens of *H. a. anatolicum*. See below.

H. anatolicum Koch; Schulze and Schlottke, 1930. Key only. Various forms synonymous with *excavatum* (sensu Delpy) keyed; for list see Tendeiro (1956, pp. 386–390) and remarks below.

H. excavatum Koch; Kratz, 1940, p. 529, synonymizes *H. excavatum* under *H. anatolicum* Koch. Description of *H. anatolicum* (pp. 529–530) is obvious mixture of both subspecies, *anatolicum* and *excavatum*, and of *H. lusitanicum*. On p. 531 reports the Koch type of *H. anatolicum* to be missing from the Zoological Institute of Munich but "those . . . of *excavatum* Koch in the Zoological Museum in Berlin"; notes especially large depressed caudal field and incomplete pons over the white parma in these specimens [the latter is an important characteristic of this subspecies, which together with the measurements and further description of Feldman-Muhsam (1954) definitely establish the identity of this form].

H. savignyi subspp. Kratz, 1940, pp. 532–536; most, though not necessarily all, of these forms (i.e., *H. savignyi* subspp., and *H. tunesiacum* subspp.) are synonymous with *H. anatolicum* subspp.

H. anatolicum anatolicum Koch; Pomerantzev, 1946, pp. 24 and 27, key descriptions of both sexes; the form referred to as *H. anatolicum excavatum* is equal to *H. anatolicum* (sensu Schulze).

H. savignyi (Gervais); Adler and Feldman-Muhsam, 1946, pp. 91–94; key to spp. in Palestine. Numerous papers by the latter author from 1947 to 1951 follow this terminology.

H. excavatum Koch; Delpy, 1946, pp. 288–293, and Delpy 1949A, pp. 103–108; key descriptions of both sexes. Delpy, 1949B, pp. 474–477, plates XIX and XX, redescriptions and illustrations of both sexes, and also synoptic lists, large parts of which represent indiscriminate lumping of species.

H. anatolicum anatolicum Koch; Pomerantzev, 1950, pp. 211–214, descriptions and illustrations of both sexes; biological data; this paper follows the systematic precedent set by Pomerantzev (1946), noted above.

H. excavatum Koch; Feldman-Muhsam, 1954, pp. 155–159; description, measurement, and illustration of Koch's type specimens; discussion; too-extensive list of synonyms.

H. excavatum Koch; Tendeiro, 1956, pp. 386–397; complete redescription and illustration of both sexes, literature review, synoptic lists.

H. anatolicum Koch; Serdyukova, 1956, pp. 79–84, key to species only.

H. excavatum Koch; Hoogstraal, 1956, pp. 435–451, 878–879, species review, including both subspecies.

H. excavatum Koch; Anastos, 1957, p. 149, literature review, including both subspecies.

Russian workers, commencing with Olenev in the 1930's, utilized the names *H. anatolicum*, *H. a. anatolicum*, and *H. anatolicum excavatum*. Not until Pomerantzev (1946, pp. 24–27, and 1950, pp. 211–214) was it possible definitely to determine exact species or subspecies in Russian literature. Most Soviet references between the late 1940's and 1954 follow the Pomerantzev system. Identified specimens presented to us in 1957 and 1958 by Russian workers conform exactly to Pomerantzev's descriptions and illustrations and to our own samples from Europe, Africa, and Asia. However, since Pervomaisky (1954) reverted to the opinion that this is a single, exceptionally polymorphic species (with which we cannot agree), Soviet workers have again dropped subspecific designations.

In order accurately to determine different authors' usage, we made a comparative study of material in the RML collections, including the Schulze collection, and in our collection, including Russian-identified specimens. We also again reviewed pertinent literature mentioned throughout this report. The results indicate beyond a doubt that: (1) *H. anatolicum anatolicum* (sensu Pomerantzev) is the form consistently referred to as *H. excavatum* by non-Soviet workers such as Delpy, Tendeiro, Feldman-Muhsam, the writers, and others during the past decade; and (2) *H. anatolicum excavatum* (sensu Pomerantzev) is the same form as *H. anatolicum* (sensu Schulze).

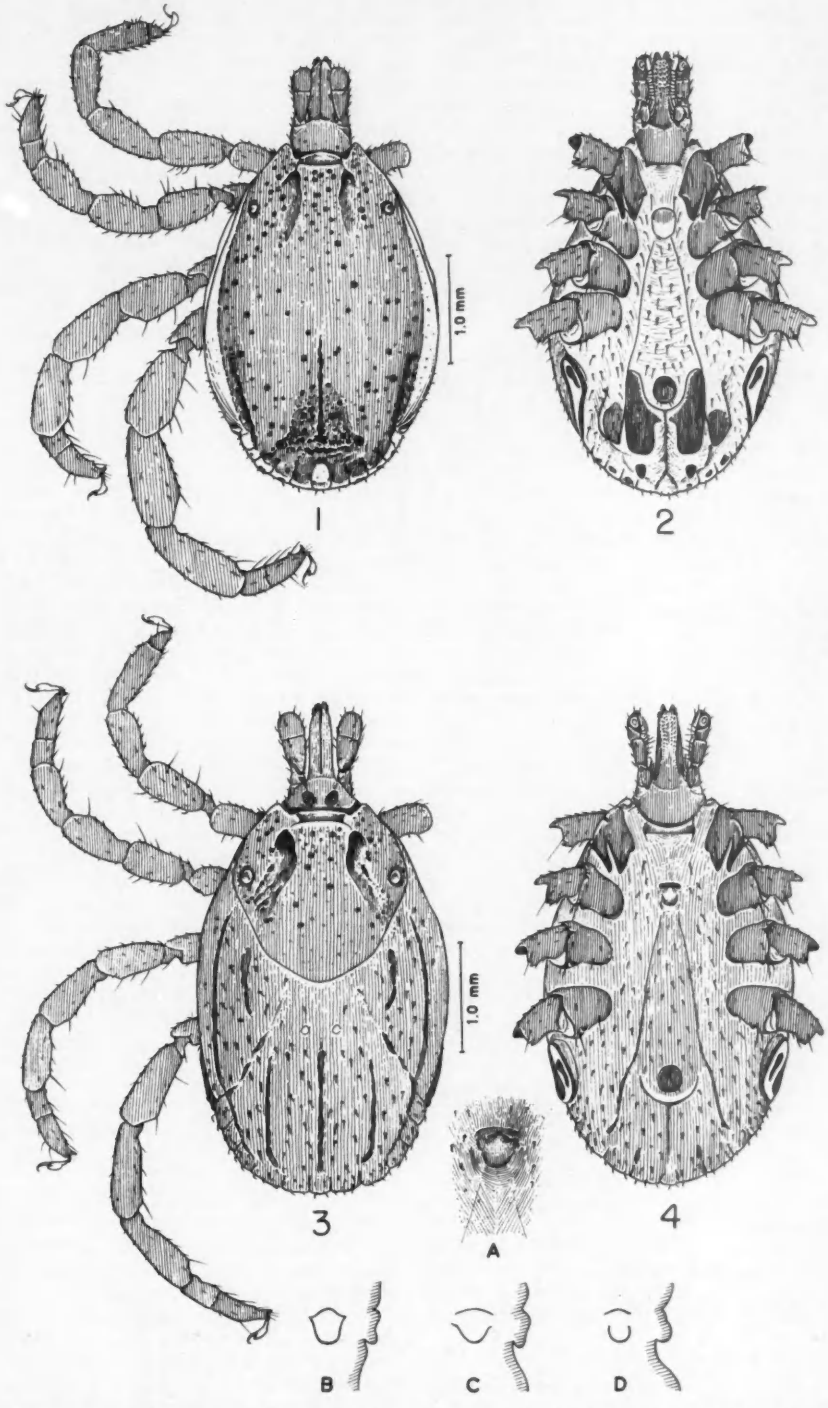
MATERIAL EXAMINED

For this study we have examined well over 10,000 specimens collected in nature in Canary Islands, Morocco, Algeria, Tunisia, Libya, Egypt, Sudan, Eritrea, Ethiopia, French Somaliland, Portugal, Italy, Palestine, Jordan, Syria, Lebanon, Turkey, Saudi Arabia, Trucial Oman, Aden, Iraq, Afghanistan, Iran, Russia, Pakistan, and India. We have also studied large series of specimens reared in the laboratory.

BIOLOGY AND DISEASE RELATIONSHIPS

H. anatolicum anatolicum has been so thoroughly reviewed in Hoogstraal (1956, pp. 435–451, 878–879) (as *H. excavatum*) that, except for the following comments and modifications, further details are not required here.

Distribution and prevalence.—Our previous summary of the distribution of this form (as *H. excavatum*) (loc. cit., pp. 437–441) stands, with the exception that it is now believed to be entirely absent in southeastern Europe, where it is replaced by *H. lusitanicum*. The same is also true in parts of or throughout Morocco and the Canary Islands. In Italy, *H. lusitanicum* is the common species except in the south (Sicily, Puglia, and Calabria) where *H. a. anatolicum* occurs (Professor O. Starkoff, personal communication). We know of no populations intergrading between *H. lusitanicum* and *H. anatolicum*



FIGS. 1–4.—*H. anatolicum anatolicum* (*sensu* Pomerantzev). ♂ and ♀, dorsal and ventral, Egypt.

subspp.; therefore the former, with its distinct morphological criteria, merits full species rank. Restudy of tremendous collections of *H. anatolicum* subspp. leads us to believe that in almost every area where it occurs the subspecies *anatolicum* is more numerous and more uniformly distributed than the subspecies *excavatum*.

Hosts and Biology.—Collation of available data reveals that *H. a. anatolicum* seldom spends any part of its life cycle on animals smaller than hares. This fact has long been maintained by Russian workers. In North Africa, at least, all stages and both sexes, especially females, are strikingly rare on animals during the coldest months of the year. Both of these findings are in direct contrast to those for *H. anatolicum excavatum*, whose immature stages are known only from small insectivores and rodents and from hares, and all of whose stages are active at all times of the year but even more so (in North Africa, at least) in winter than in summer. After more systematic biological studies in other areas where the subspecies *anatolicum* occurs, various conclusions in the previous review (loc. cit., pp. 441–448) may or may not have to be modified.

Remarks.—In the previous review (loc. cit., pp. 448–449) notes concerning Schulze's theories of leg ornamentation and Yalvac's report from Kenya probably refer actually to the subspecies *excavatum* and not to *anatolicum*.

Disease Relations.—It appears that the following sections of the previous review (loc. cit., pp. 449–450) refer to the subspecies *excavatum* and not to *anatolicum:* (1) experimental work with "*H. turkmeniense*" on Russian spring-summer encephalitis and on Russian and Japanese mosquito-borne encephalitis viruses, and (2) experimental work on survival of spirochetes in Russia. Also, remarks concerning infection with *Coxiellia burnetii* in southern Europe and in Morocco refer entirely or partly to *H. lusitanicum*.

IDENTIFICATION

The previous description of this form (loc. cit., pp. 450–451) stands except that most of the "atypical" specimens mentioned therein are now found to represent *H. anatolicum excavatum*. Owing to the fact that a neotype of *H. a. anatolicum* is reported in the present paper, this form is redescribed below.

Males.—Small, yellowish-brown ticks, with a convex, lightly punctated scutum; very short but distinct lateral grooves; a depressed punctate caudal field between two smooth ridges; a pronounced posteromedian groove not reaching the parma; small subanal shields directly posterior of adanal shields; legs yellowish, unstriped, rarely with faint pale markings, but not marbled when dry.

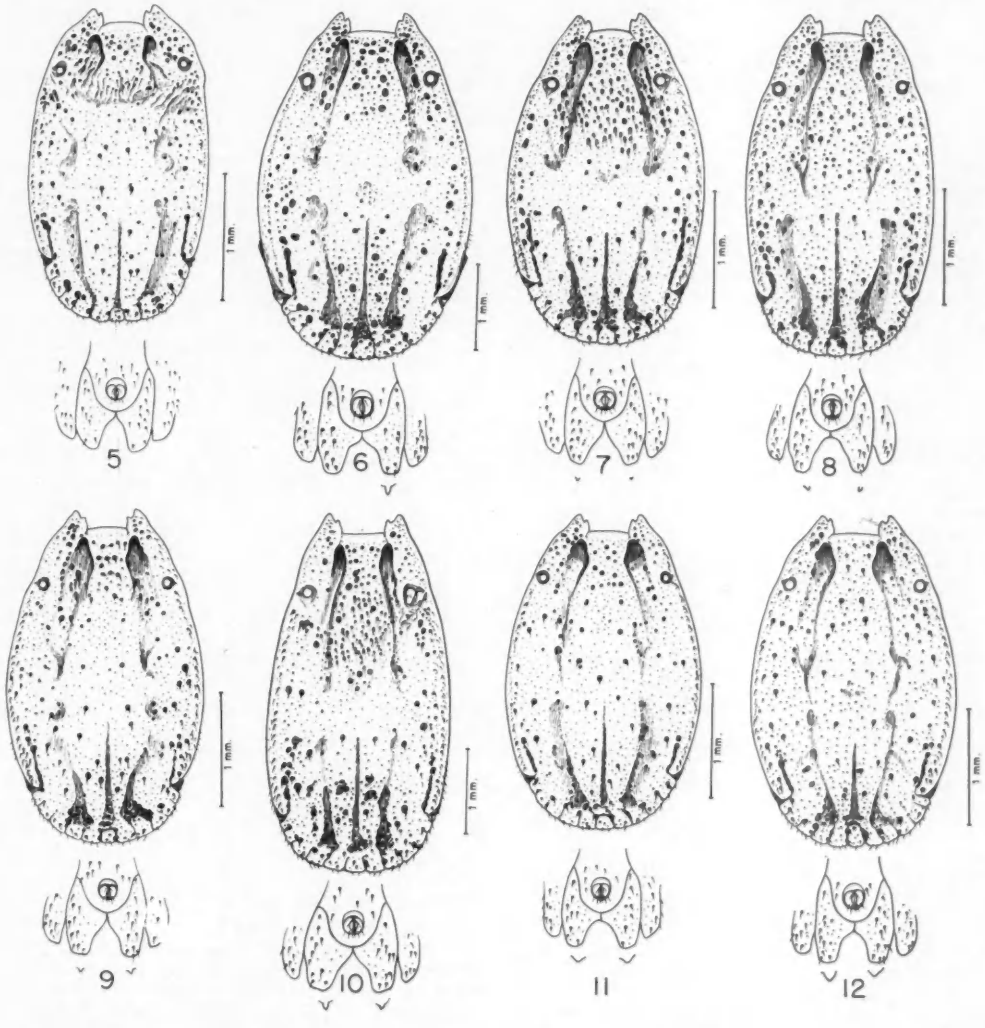
The scutum measures no more than 3.85 mm. in length and 2.33 mm. in width. Average specimens are 3.50 mm. in length and 2.00 mm. in width, but smaller individuals and populations are common locally or seasonally. Typical color is yellowish brown becoming darker reddish brown on larger specimens. Cervical grooves are superficial, comparatively short, not extending beyond anterior third of scutum if that far. Lateral grooves are very short, deep, distinct, a row of closely spaced large and/or small punctations may continue anteriorly from them. The posteromedian groove is pronounced; it is separated from the parma by a group of warts or by a narrow smooth area. Paramedian grooves are rather superficial, bordering the inner side of the very slight lateral ridges bounding the depressed caudal area. The caudal field has large punctations, but these are few and non-contiguous, and small punctations. The smooth, convex scutum has very few large, widely spaced, shallow punctations and a varying number of superficial minute punctations; punctations are somewhat more dense between cervical grooves and on scapulae. The parma is a paler color than the scutum; it is almost invariably present. The pair of festoons bordering the parma (paraparmal festoons) are elevated and slightly extended anteriorly, the next pair end at the paramedian grooves, and the two lateral pairs are fused into the lateral ridges. Subanal shields (figures 5–12) are small to minute, usually elongate, not infrequently one or both are lacking (see below); they are borne directly posterior of the adanal shields but in either hugely engorged individuals or in freshly molted and preserved individuals they may be more or less laterally displaced on udderlike swellings. The legs are yellowish or pale brown, not striped, rarely with faint pale markings, not marbled when dry.

For intraspecific intergradation, see section below. Some populations, especially all of those that we have seen from India, are very small, measuring a maximum of 3.10 mm. in scutal length. Populations from far eastern Turkey (Lake Van), Caucasus (U.S.S.R.), Afghanistan, Pakistan, and India have exaggeratedly narrow scutums, measuring 3.60 mm. in length and only 1.95 mm. in width. It is strongly suspected that these may eventually prove to be a separate subspecies of the *anatolicum* complex. We have recently commenced rearing pertinent material to determine its biological and taxonomic status, an effort that will require at least a year to complete.

Variation in subanal shields.—Figures 5 to 12 lucidly illustrate variation in subanal shields of this subspecies. In figures 10 and 11, subanal shields are of normal size, in figure 12 they are somewhat larger than usual, in figures 7 to 9 they are minute to small, in figure 6 only one is present, and in figure 5, none is present. This small sample from a series of over 100 reared by the writers from nymphs from cattle at Ankara, Turkey, is representative of variation in numerous

large collections of *H. a. anatolicum*. Pomerantzev (1950, p. 214) has similarly noted that "among collections of *H. a. anatolicum* modified forms are frequently found with weak scutal shields and reduced anal shields and aprons; this phenomenon is observed chiefly in the Ararat valley of Armenia where this subspecies appears in masses." Specimens lacking subanal shields are also found in collections of *H. truncatum*, *H. marginatum*, and other *Hyalomma* species. Unfortunately, overeager taxonomists with small samples to work with have applied species names to these abnormal individuals (see *Discussion* below).

Females.—The knoblike genital apron is always definitely bulging in profile; in outline it may be circular, elongately triangular, or (in greatly engorged specimens only) widely triangular (but if so, always distinctly smaller than in *H. marginatum* or similar species). The circular outline is most characteristic and distinctive; the elongately triangular outline is fairly common and usually fairly distinctive; the uncommon widely triangular outline may be confusing. Scutal color varies from yellowish brown to dark brown in larger specimens and is usually darkest in the scapular areas. The scutum, almost invariably



FIGS. 5–12.—*H. anatolicum anatolicum* (*sensu* Pomerantzev). ♂♂ scutums and associated posterior ventral surfaces to show variation in and absence of subanal shields. Material reared by authors at Ankara, Turkey, 1954, from nymphs from cattle.

longer than wide, measures a maximum of 2.00 mm. in length and 1.90 mm. in width; average specimens are 1.90 mm. in length and 1.71 mm. in width; the posterior margin is always narrowly rather than widely rounded. The scutum has few large punctations scattered in the central field, a few more in the scapular areas, and some to many very fine, superficial punctations over much of the surface. The legs are yellowish brown, either very faintly striped or unstriped. Typical engorged females are comparatively small and narrowly elongate but quite thick dorsoventrally, thus presenting a narrowly rectangular appearance.

COMPARISON OF THE SUBSPECIES *anatolicum* AND *excavatum*

H. a. anatolicum	*H. anatolicum excavatum*
MALES	
Small, frail, pale ticks; scutal length up to 3.85 mm., usually less, NEVER MORE	large, robust, dark ticks; scutal length 4.00 to 6.00 mm.; seldom less
Color pale to pale reddish brown	reddish brown to dark brown
Central punctations not deep	deeper
Caudal depression usually with some large punctations	with many small, seldom large punctations
Posteromedian groove separated from parma by narrow smooth or warty area	by bridgelike extension or usually fusion of paraparmal festoons
Ridges beside caudal field weakly elevated if at all	distinctly elevated
Adanal shields weakly chitinized, margins almost straight externally and rounded apically	heavily chitinized, margins convex externally and usually rectangular apically
Subanal shields elongate, weakly chitinized, often rudimentary or absent	less elongate, heavily chitinized, seldom if ever rudimentary or absent
Legs yellowish or pale brown, not striped, never marbled when dry	legs light brown, sometimes faintly striped, usually marbled when dry
FEMALES	
Scutal length less than 2.00 mm.	usually more than 2.00 mm.
Color yellowish brown to brown	reddish brown to dark brown
Genital apron outline circular or elongately triangular; widely triangular only when engorged	outline typically widely triangular, also may be circular or elongately triangular
Scutum weakly chitinized, large punctations not deep	heavily chitinized, large punctations deeper
Legs faintly striped with pale yellowish - brown rings; never marbled	faint reddish brown rings, usually marbled when dry
BIOLOGY	
Adults and immature stages seldom on hosts in winter (North Africa)	both sexes commonly on hosts in winter
Immature stages chiefly on larger domestic animals or wild animals no smaller than hares	known only from small insectivores and rodents, and hares
Distribution generalized	localized

NEOTYPE

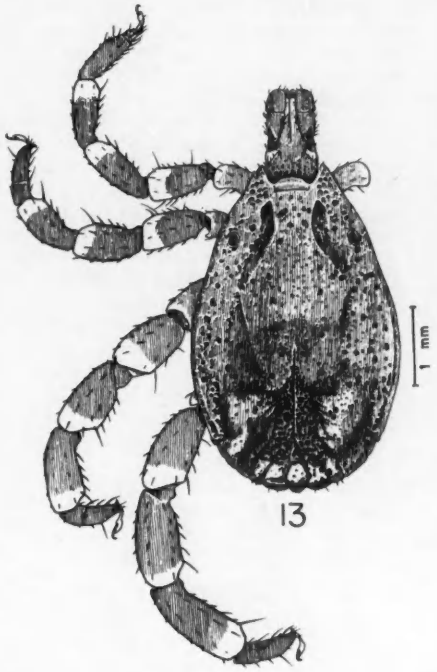
Inasmuch as it has been definitely established by Kratz (1940) and Feldman-Muhsam (1954) that the type specimen of *H. anatolicum* is lost, a neotype male of *H. anatolicum anatolicum* Koch, 1844, bearing the following data, "cattle, abattoir, Iskenderun, Turkey, 12 August 1954, H. Hoogstraal and M. N. Kaiser, collectors," has been selected and deposited in the United States National Museum together with a female bearing the same data. In addition, two males and one female bearing the same data are deposited in the following collections: Veterinary Faculty of Ankara University, Rocky Mountain Laboratory, Chicago Natural History Museum, American Museum of Natural History, Department of Zoology of University of Maryland, British Museum (Natural History), Institute of Malariology and Parasitology (Moscow), Academy of Science (Leningrad), Museum National d'Histoire Naturelle (Paris), Centro de Zoologia (Lisbon), Institute of Parasitology (University of Rome), Institutes Pasteur in Tunis, Alger, and Casablanca, Entomological Society of Egypt, East African Veterinary Research Organization (Muguga), Division of Veterinary Services (Onderstepoort), the writers, and others.

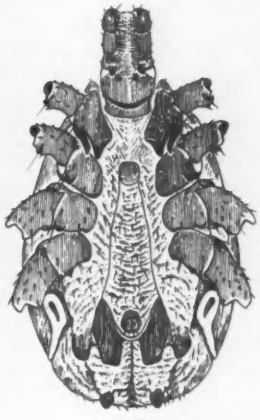
The neotype male is described above, under Identification, together with others in the same lot. The neotype male scutum measures 3.50 mm. in length and 2.00 mm. in width; the scutum of its associated female measures 1.90 mm. in length and 1.71 mm. in width.

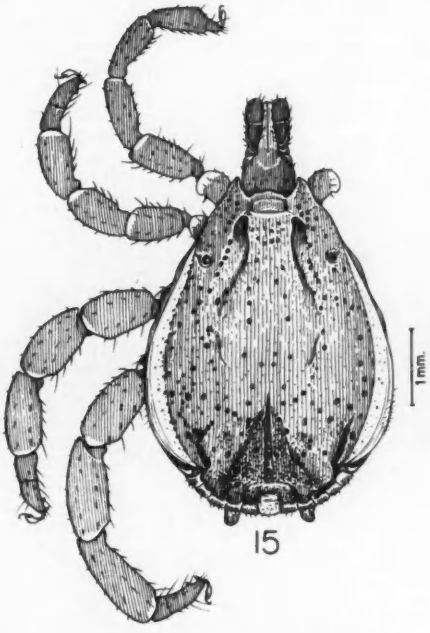
In accordance with the International Rules of Zoological Nomenclature, approval for selection of this neotype has been obtained from the following ixodid specialists: Drs. C. B. Philip and G. M. Kohls (Hamilton), J. Tendeiro (Lisbon), O. Starkoff (Rome), and G. Theiler (Onderstepoort). Professor Serdyukova, however, declined comment except to refer to recent Soviet opinion [i.e. Pervomaisky (1954)]. A copy of the manuscript was sent to Dr. Francis Hemming, Secretary of the International Commission of Zoological Nomenclature, seven months before being submitted for publication.

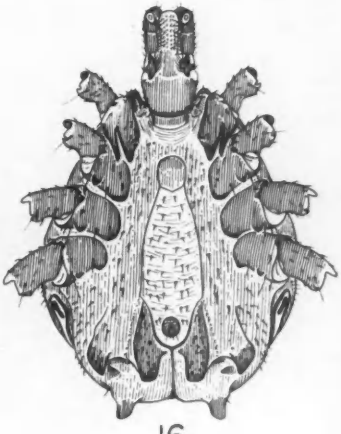
SUBSPECIFIC INTERGRADATION

As noted above, we have studied well over 10,000 specimens of *H. a. anatolicum* from 26 countries and territories ranging from the Atlantic coast of North Africa to India. In many of these areas, all available specimens are morphologically strictly representative of their own subspecies and can be identified with certainty. In certain areas, a small to moderate degree of random overlap occurs between populations of the two subspecies. In Egypt, this hybridization amounts to somewhat less than 20 percent in populations on the Mediterranean littoral, 5 to 10 percent in the Lower Nile Valley and Delta, and none in









FIGS. 13–14.—*H. anatolicum excavatum* (*sensu* Pomerantzev). ♂, dorsal and ventral, heavily punctate, not engorged (subanal shields normal), Egypt.

FIGS. 15–16.—*H. anatolicum excavatum* (*sensu* Pomerantzev). ♂, dorsal and ventral, punctate, not normally engorged (subanal shields displaced), Egypt.

Upper Egypt. In Turkey, it is approximately 2 percent throughout the Anatolian highlands to the eastern boundaries of the country but reaches approximately 5 percent in the lowlands around Iskenderun, near Syria. In Libya, it is somewhat less than 20 percent in our numerous samples, mostly from the Mediterranean littoral. In other areas from which we have large representative collections, i.e., Sudan, French Somaliland, Yemen, eastern Saudi Arabia, and Iraq, and in others from which our samples are smaller, no overlap has been observed.

Intergrading males are of intermediate size, from approximately 3.65 to 4.10 mm. in scutal length, the posteromedian and paramedian grooves are more pronounced than in the larger subspecies (i.e., ***anatolicum***), the legs are reddish, and the scutal color is variable between the two subspecies. Females are also intermediate in size, their scutum measuring from approximately 1.85 to 2.15 mm. in length, and their legs being variable in color.

Hyalomma (Hyalomma) anatolicum excavatum Koch

The Large Anatolian Hyalomma

(Figures 13–19, 24)

Hyalomma excavatum Koch, 1844, p. 222, short description of ♂ from Egypt. Kratz (1940) reported the type specimen(?s) to be in the Zoological Museum of Berlin and Feldman-Muhsam (1954) reported a single type male in the Schulze collection. Where this specimen is presently deposited is not certain.

H. excavatum Koch; Koch, 1847, pp. 14, 45–46, Plate VI, Fig. 22, ♂ redescribed and illustrated.

H. anatolicum Koch; Schulze and Schlottke, 1930, pp. 36 and 44, keys to both sexes.

H. anatolicum zavattarii n. subsp., Tonelli-Rondelli, 1935, pp. 240–242, fig. 1, description and illustration of ♂ from Murzuch, Fezzan, Libya. We consider this to be a synonym of *H. anatolicum excavatum*.

H. anatolicum anatolicum Koch; Kratz, 1940, pp. 529–531, figs. 12–14; descriptions and illustrations of both sexes from material in Schulze collection.

H. anatolicum excavatum Koch; Pomerantzev, 1946, pp. 24 and 27, new combination, key to both sexes.

H. excavatum Koch; Delpy, 1949B, pp. 475, 485, 486, new synonymy; no reference to type material.

H. anatolicum excavatum Koch; Pomerantzev, 1950, p. 214, short comparative description of ♂; synonymy of *H. turkmeniense* Olenev, 1932 (sic; should be 1931) under this name.

H. excavatum Koch; Feldman-Muhsam, 1954, pp. 155–159, description and illustration of type specimen, synoptic list; Schulze collection specimens (of both subspecies) considered to be "within range of variation of *H. excavatum*."

H. excavatum Koch; Tendeiro, 1956, pp. 386–389, descriptions and illustrations of both sexes, separation of *H. lusitanicum*; synoptic list.

H. excavatum Koch and *H.* sp. no. 2 near *excavatum*; Hoogstraal, 1956, pp. 435–451, 878–879, 884–887.

H. anatolicum Koch; Serdyukova, 1956, pp. 79–84; key to species only.

H. excavatum Koch; Anastos, 1957, p. 149, literature review including both subspecies.

A very few non-Soviet students referred to the present subspecies as *H. anatolicum* following the work of Schulze and Schlottke (1930), which amounted merely to a key to species. Material in the Schulze collection was elucidated by Kratz (1940, pp. 529–531) who redescribed both sexes and illustrated (figures 1, 12–14) the *H. anatolicum* specimens in this collection from southern Europe, the Near East, Middle Asia, Northwest Africa, and East Africa (i.e. Kenya). Kratz very likely confused several specimens of other species in the material he described. Tonelli-Rondelli (1932B, p. 373) reported a specimen from Libya and also described (1935) the synonymous subspecies *zavattarii* from Somalia. Bodenheimer (1937, p. 244) noted the presence of this form in Palestine. Various authors listed by Hoogstraal (1956, p. 438) have reported *H. anatolicum* from Kenya. [To our surprise we found an accurately determined specimen labelled Kabete, Kenya, in the Schulze collection. This Kenya sample was probably from a temporary population resulting from an adventitious introduction.] All of these 1930–40 workers were students of or in correspondence with Professor Schulze.

MATERIAL EXAMINED

Total.—Approximately 6,000 specimens collected in nature and numerous others reared in the laboratory. Owing to the negligible amount of previous information concerning this subspecies, all available locality data and host and month of collection data are presented below. Because of its historical importance, material in the Schulze collection is listed separately.

Schulze collection.—The following specimens, now in the Schulze collection in the Rocky Mountain Laboratory, bear Schulze's labels of *H. anatolicum* and are typical of *H. anatolicum excavatum*. (Areas in parentheses are our additions; other words in parentheses are illegible). 15 ♂♂ [Usak, Anat(olia) (Turkey) Heint]. 22 ♂♂, 1 ♀ [Rind, Usak, Anat(olia) (Turkey) Steiner leg.]. 10 ♂♂, 13 ♀♀ [*Bos taurus*. Ins. Skyros (Skiros Island, Greece), leg. Stepanides, Apr. 10, 1936]. 4 ♀♀ [*Bos taurus*, Ins. Skyros (Skiros Island, Greece), Aug. 10, 1935]. 3 ♂♂, 3♀♀ [*Ovis aries*, Ins. Skyros (Skiros Island, Greece), Stephanidis leg., Aug. 10, 1935]. 1♂, 1♀ [15 *Ovis aries*, Ins. Thassos (Thasos Island, Greece), leg. Kanellis, Aug. 6, 1935]. 5 ♂♂ [Pferd. Maz. (? Macedonia, Greece)]. 2 ♂♂, 1♀ [Maz. (? Macedonia, Greece)]. 1 ♂ [Cerniste, Maz. (? Macedonia, Greece). *Nuttallia equi* 18.6.17]. 1♂ [Zecke von Kamel, Kairo (Egypt), Dr. med. E. Bannworth leg., vend. 1.IX.1913]. 4 ♀♀ [Pferd. Kazakstan, Stadt. Turkestan (Russia), N. Olenev leg. 2.VI.1929]. 1 ♂ [37. Kabete, Kenya]. 1 ♂, 5 ♀♀ [Rio d'Oro (Spanish Sahara) P. Gratz L.V. (? Mendas antilope)]. 1 ♀ [Rio d'Oro (Spanish Sahara), Spasr G.V.I.N. G.2250/26)]. 14 ♂♂ [Rind,

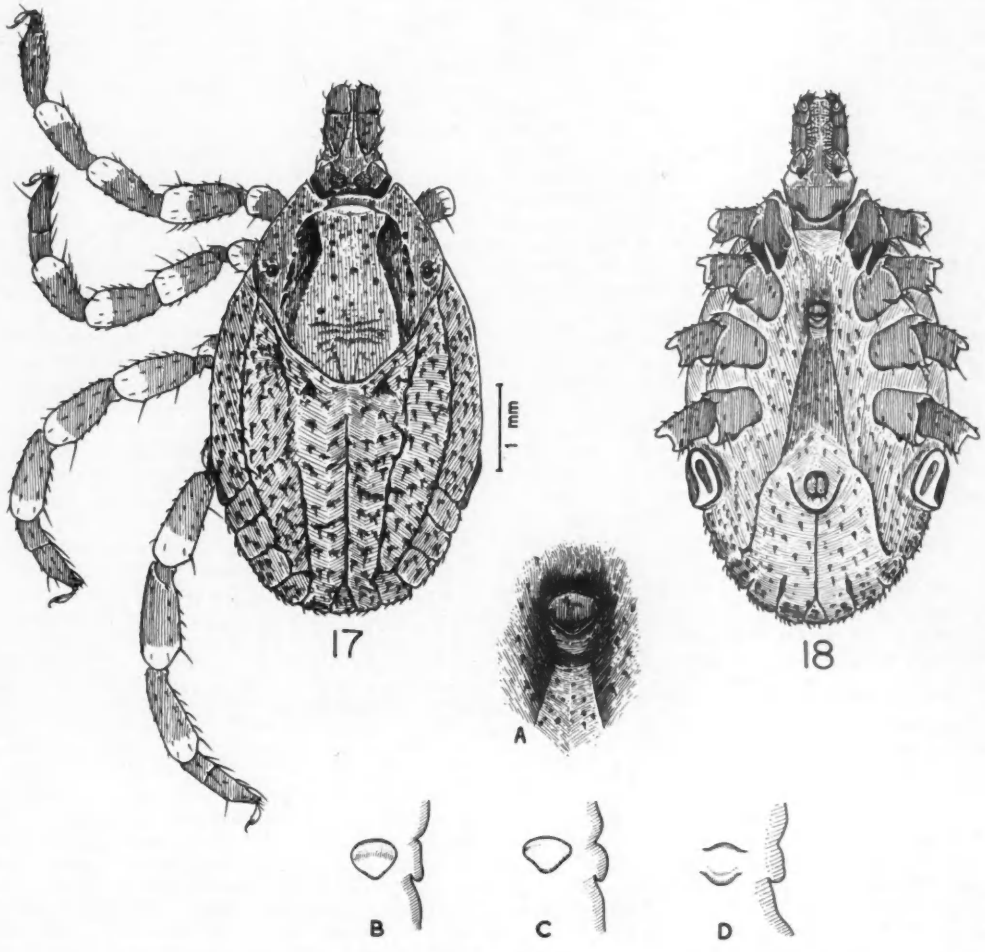
Novo Selo (? Nuvo Sels or Nuvs Lels) 15/10]. 1 ♀ [Perniga (? Perugia)]. 1 ♂ [Hudova, Mared (? Hutova, Maret), Fehringer].

Also in the Schulze collection are the following specimens, labelled as *H. tunesiacum* subspp., which are typical of *H. a. anatolicum* [for further details see Hoogstraal and Kaiser, 1958b.] 2 ♂♂, dog and sheep, Agordat, Eritrea, spring, 1931 (cotypes of synonymous *H. tunesiacum ganorai* Tonelli-Rondelli). 1 ♂, Arak River, Transcaucasia, 1 January 1906.

KNOWN DISTRIBUTION

SPANISH SAHARA. Schulze collection, no locality. MOROCCO. Mogador (BMNH). ALGERIA. Specimens in Tendeiro collection from Institut Pasteur d'Algérie (personal communication). TUNISIA. Tunis (Schulze collection; probably type of *H. tunesiacum* Sc. & Sc.). LIBYA (CYRENAICA). 3 to 5 kilometers west of El Agheila; Ghemines, Gardinia, and Beneina (all NAMRU3). (TRIPOLITANIA.) Specimens in Tendeiro collection (personal communication). See also records from Libyan camels in Egypt.

EGYPT. *Western Desert Governorate:* Siwa Oasis, Salum, Bir Bosslanga near Salum, Mersa Matruh, El Alamein, El Hammam, Burg El Arab, Bahig, El Amiriya, Wadi Natroun. *Cairo Governorate:* Cairo (transient animals and others in abattoir). *Red Sea Governorate:* near Cairo, near Zagazig, Ain Sukhna, Wadi Bikheit, and St. Anthony's Monastery (Wadi Araba). *Southern Desert Governorate:* Bir Abraq. *Sinai Governorate:* Feiran Oasis, Wadi Feiran, St. Catherine's Monastery



FIGS. 17–18.—*H. anatolicum excavatum* (*sensu* Pomerantzev). ♀, dorsal and ventral, Egypt.

(5,000 feet elevation), El Arish, Kosaima. *Introduced into Egypt:* Cairo abattoir (numerous ♂♂ on camels and cattle said to originate in the Sudan, and on cattle said to originate in "East Africa," possibly Somaliland or Ethiopia). Alexandria Quarantine Station (♂♂ on camels from Libya). Salum Frontier Station and El Hammam market (numerous ♂♂ and ♀♀ on camels from Libya). See also Schulze collection data above. Note absence in Nile Valley and Delta.

SUDAN. Kassala, Kassala. ETHIOPIA (ERITREA). Agordat (Schulze collection, as *H. tunesiacum ganorai* Tonelli-Rondelli). FRENCH SOMALILAND. Plaine de Haule, Ali Sabiet, and Djibouti (HH). KENYA. Kabete (Schulze collection, probably from a nonestablished, adventitiously introduced population).

YEMEN. Ta'izz (HH). PALESTINE. Jaffa and Gaza (BMNH and NAMRU3).

CRETE. (Schulze collection, "probably *H. tunesiacum* Sc. & Sc."—note by Kohls.) GREECE. Macedonia and Skyros (Skiros) and Thasos (Thassos) Islands (Schulze collection).

TURKEY. Usak (Kutahya) (Schulze collection). Istanbul and Ankara abattoirs, Kara Kopru (Urfa), and Iskenderun (Hatay) (HH & MNK). Ayvalik, Kurktoy, Nesbiye, Kadirli, and Asayiciyanli (Ceyhan), Gocer (Maras) (NAMRU3). Kirklareli (Kirklareli), Bursa (Bursa), Manyas (Balikesir), Salihli (Manisa), Nazilli (Aydin), Bodrum (Mugla), Saraykoy and Acipayam (Denizli), Ladik (Samsum), Niksar (Tokat), Amasya (Amasya), Tarsus (Icel), Hassa, Reyhanli, and Dortyol (Hatay), Birecik (Urfa), Kulp (Diyarbakir) (RML). In Turkey this form ranges from the Greek and Bulgarian frontiers at least to longitude 40°E. and is common locally in the lowlands and foothills near the Black and Mediterranean Seas but rare on the high Anatolian steppes and in the mountains of the old Kurdistan area.

U.S.S.R. Kazakh S.S.R. (Schulze collection). Specimens in HH collection lack locality labels. [According to Pomerantzev (1950, p. 214) this subspecies occurs in Turkmen S.S.R., southern Kazakh S.S.R., and Tazhik S.S.R. IRAN. Pomerantzev (*loc. cit.*) states that this form also occurs in Iran].

HOSTS OF ADULTS AND MONTH OF COLLECTION

SPANISH SAHARA. Antelope: 1 ♂, 5 ♀♀. MOROCCO. Cattle: 11 ♂♂, 7 ♀♀. LIBYA. Camels: 25 ♂♂, 12 ♀♀ (October). Goats: 1 ♂, 3 ♀♀ (April), 4 ♂♂, 2 ♀♀ (October). Cattle: 4 ♂♂, 4 ♀♀ (November). Sheep: 1 ♂, 4 ♀♀ (November). On ground: 2 ♂♂ (October).

EGYPT. Man: 1 ♂ (March). Camels: 2 ♂♂ (January), 93 ♂♂, 10 ♀♀ (February), 49 ♂♂, 5 ♀♀ (March), 21 ♂♂, 11 ♀♀ (May), 11 ♂♂, 6 ♀♀ (June), 1 ♂ (July), 87 ♂♂, 22 ♀♀ (October), 8 ♂♂, 1 ♀ (December) (see also market camels below). Cattle: 24 ♂♂, 11 ♀♀ (January), 1 ♂ (September). Donkeys: 52 ♂♂, 13 ♀♀ (March). Sheep: 8 ♂♂, 3 ♀♀ (December), 32 ♂♂, 15 ♀♀ (January), 19 ♂♂, 11 ♀♀ (February), 1 ♂, 2 ♀♀ (March), 2 ♂♂, 3 ♀♀ (April), 16 ♂♂, 4 ♀♀ (August), 35 ♂♂, 10 ♀♀ (October). Goats: 4 ♂♂ (February), 7 ♂♂ (May). On ground: 1 ♀ (October). On ground in camel yard: 4 ♂♂, 7 ♀♀ (October), 68 ♀♀ (February). On ground, desert: 1 ♀ (October). On abattoir animals from foreign countries: 4 ♂♂ (January), 39 ♂♂ (February), 1 ♂, 5 ♀♀ (October), 39 ♂♂ (November). On Libyan camels at Salum Frontier Station: 2 ♂♂, 1 ♀ (October). On Libyan camels (10 each month) at El Hammam market: 69 ♂♂, 220 ♀♀ (December), 235 ♂♂, 285 ♀♀ (January), 237 ♂♂, 197 ♀♀ (February), 145 ♂♂, 412 ♀♀ (March), 110 ♂♂, 797 ♀♀ (April), 169 ♂♂, 494 ♀♀ (May) (no June collections), 168 ♂♂, 501 ♀♀ (July), 140 ♂♂, 372 ♀♀ (August).

SUDAN. Camel: 1♂, 4♀♀ (May). ERITREA. Dog and sheep: 2 ♂♂ (spring). FRENCH SOMALILAND. Camels: 4 ♂♂, 2 ♀♀ (July). Cattle: 1 ♂ (July). Sheep: 2 ♂♂ (July). Goats: 1 ♂ (July).

YEMEN. Camels: 10 ♂♂, 1 ♀ (February). Cattle: 9 ♂♂, 5 ♀♀ (February). PALESTINE. Cow: 1 ♂ (June). Camel: 8 ♂♂, 1 ♀ (July).

CRETE. No Host: 1 ♂ (June). GREECE. Cattle: 10 ♂♂, 13 ♀♀ (April), 4 ♀♀ (August). Horse: 5 ♂♂ (no month). Sheep: 4 ♂♂, 4 ♀♀ (August).

TURKEY. Cattle: 50 ♂♂, 17 ♀♀ (no month), 6 ♂♂, 17 ♀♀ (June), 2 ♂♂, 14 ♀♀ (July), 41 ♂♂, 7 ♀♀ (August), 11 ♂♂ (September). Sheep: 1 ♂ (September). Horses: 8 ♂♂, 18 ♀♀. Donkeys: 3 ♂♂, 1 ♀. Mule: 2 ♂♂. Goats: 16 ♂♂, 11 ♀♀. Buffaloes: 4 ♂♂, 4 ♀♀. Camels: 6 ♂♂.

RUSSIA. Horse (Schulze collection). No hosts or seasonal data are reported by Pomerantzev (1950) or recorded on labels of Russian material in HH collection.

In summary, camels and cattle appear to be usually the most consistent and heavily infested hosts. Sheep, goats, and horses may be somewhat less important hosts, and domestic buffaloes, donkeys, mules, man, dogs, and antelopes serve as occasional hosts. The rate of infestation varies with locality and season and more careful studies on this subject are obviously required.

HOSTS OF NYMPHS (EGYPT)

The following are the data for adults of *H. anatolicum excavatum* that we have reared from nymphs in Egypt. We are unaware of any other published data for the immature stages of this form. In the paragraphs below, the hosts' scientific and common names are listed together with the locality and time of collecting. In the field it was not always possible to observe the exact date that nymphs dropped from the host or molted to adults.

Paraechinus d. dorsalis (Anderson and de Winton, 1901), Arabian Paraechine Hedgehog. Wadi Feiran, Sinai, adults reared from nymphs collected on 21 May 1953 and from St. Catherine's Monastery on 24 and 26 May 1958.

Hemiechinus auritus libycus (Ehrenberg, 1833), Libyan Long-eared Hedgehog, Burg El Arab, Western Desert; nymphs disengaged from host on 22 October, molted to adults on 17 November; other newly molted, unengorged adults from burrows of this form of hedgehog 70 miles east of Mersa Matruh, Western Desert, 22 September.

Hemiechinus auritus metwallyi Setzer, 1957, Nile Delta Long-eared Hedgehog. Various localities in Beheira Province, adults reared from nymphs from hosts taken in May, September, and November.

Lepus capensis rothschildi de Winton, 1902, Rothschild's Hare. Seacoast 4 miles east of Libyan frontier, nymphs collected in October 1953.

Jaculus j. jaculus (Linnaeus, 1758), Common Lesser Jerboa. 12 miles east of El Amiriya, Mariut, Western Desert, nymph dropped 29 October 1954, molted on 30 November.

Acomys russatus (Wagner, 1840), Golden Spiny Mouse. 8 adult ticks reared from nymphs at St. Catherine's Monastery (5,000 feet altitude), Sinai, November 1952.

Gerbillus (*G.*) *gerbillus gerbillus* Olivier, 1801, Egyptian Lesser Gerbil. 5 adult ticks reared from nymphs from hosts from the desert fringe west of Cairo.

Meriones c. crassus Sundevall, 1842, Eastern Desert Jird. Midway between Cairo and Suez, adults reared from nymphs taken 12 April 1953, 24 October 1957, and 23 January 1958.

Meriones crassus pallidus Bonhote, 1912, Pale Jird. Female from nymph, Bir Abraq, Southeastern Desert, February 1954.

Psammomys o. obesus Cretzschmar, 1828, Fat Sand-rat. Several unengorged, newly molted adults from burrows in the Eastern Desert 29 kilometers east of Cairo (17 December 1954), at Hafs, Damanhur, Beheira and in the Western Desert at Mersa Matruh (9 November 1953, 23 September 1954 and 21 September 1957); in addition 15 adults were reared from nymphs that dropped from fat sand-rats at several of the localities noted above.

"Rodent burrows." Several unengorged, newly molted adults from Wadi Nasuri, Eastern Desert, and Libyan Plateau overlooking Salum, Western Desert (October 1953).

LIFE CYCLE

Rearing experiments (with the technical assistance of Sobhy Gaber) indicate that *H. anatolicum excavatum* may undergo either a two-host or three-host type of life cycle. An engorged female removed from a camel at Abu Rawash, Giza, Egypt, on 23 May 1957, and held at Cairo summer room temperature, commenced oviposition on 1 June; these eggs hatched on 27 June. On 31 July, 292 larvae from this batch were placed on the ear of a rabbit. On 3 August, 151 of these larvae detached and molted to nymphs on 8 August; they were then preserved for morphological study. However, 141 larvae remained on the host and molted to nymphs. After feeding, 43 of these nymphs detached on 12 August and molted to 22 males and 21 females on 26 August; 49 detached on 13 August and molted to 36 males and 13 females on 28 August; 31 detached on 15 August and molted to 12 males and 19 females on 29 August; 18 detached on 16 August and molted to 6 males and 12 females on 30 August.

In summary, 27 days are required for hatching of eggs held in humidified tubes at Cairo summer room temperature. Of 292 larvae secured from a single egg batch, 151 detached from the rabbit host after 4 days of feeding and molted to nymphs 5 days later (three-host type of life cycle); they were then preserved. A slightly smaller number of larvae, 141, underwent a two-host type of life cycle, remaining on the same host, feeding, molting to nymphs, feeding again, and then detaching from 13 to 17 days after having been placed on the host as unfed larvae. These individuals molted to 76 males and 65 females 14 or 15 days after having detached as engorged nymphs. Assuming the prefeeding period of newly hatched larvae to be 4 days, 58 to 63 days are necessary to complete the two-host cycle from oviposition to appearance of adults under conditions described above. Life cycle studies of subsequent generations are presently underway.

During the winter, spring, and summer of 1958, after the main body of this manuscript was completed, we have been rearing the progeny of individual females of both subspecies of *H. anatolicum* (and of *H. lusitanicum*) on a variety of hosts. The results, even in the F_2 generation, contain no evidence to suggest that these are not two distinct biological and taxonomic entities. Indeed, the individual morphological characteristics of the immature stages have proved to be even more distinct than we had thought might be possible. The results of this study will be presented in a separate report in the present series.

IDENTIFICATION

The description of *H.* sp. no. 2 near *excavatum* (Hoogstraal, 1956, pp. 886–887) is herein expanded to provide more precise definition of this subspecies.

Males.—Medium-size to large ticks usually measuring from 4.00 to 5.12 mm. (or larger) in length and from 2.55 to 3.55 mm. (or more) in width; average specimen 4.50 mm. in length and 2.95 mm. in width. Individuals and limited populations ranging somewhat smaller than these dimensions can usually be readily distinguished from the related subspecies by morphological

criteria. Color is shiny dark brown or reddish brown. The caudal depression has numerous, often contiguous, small punctations, large punctations are usually absent in this depression but may be present in very robust, comparatively heavily punctate individuals. The shallow posteromedian groove is separated from the white or pale parma by a slightly elevated pons formed by the anterior extension and sometimes fusion of the paraparmal festoons; the caudal depression is bounded laterally by distinctly elevated ridges. The shallow cervical grooves extend at least to or beyond the anterior third of the scutum. Large punctations in the central field are deeper than in the subspecies *anatolicum* but the scutal surface appears smoother than in that subspecies. The adanal shields are more heavily chitinized, their external margin is usually rectangular; their outer margin is convex, usually strongly so. The subanal shields are larger and more heavily chitinized than in the subspecies *anatolicum* and none have been observed to be rudimentary or absent. The light or yellowish brown legs are sometimes faintly striped and usually marbled when dry.

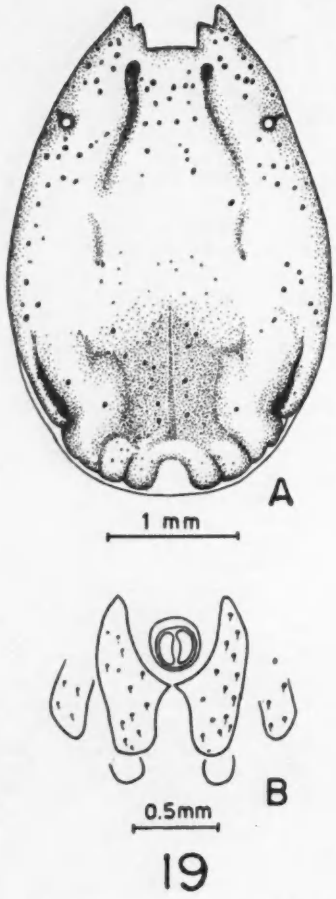


FIG. 19.—Type specimen of *H. excavatum* Koch, 1844 (After Feldman-Muhsam, 1954). A. Scutum. B. Posterior ventral surface.

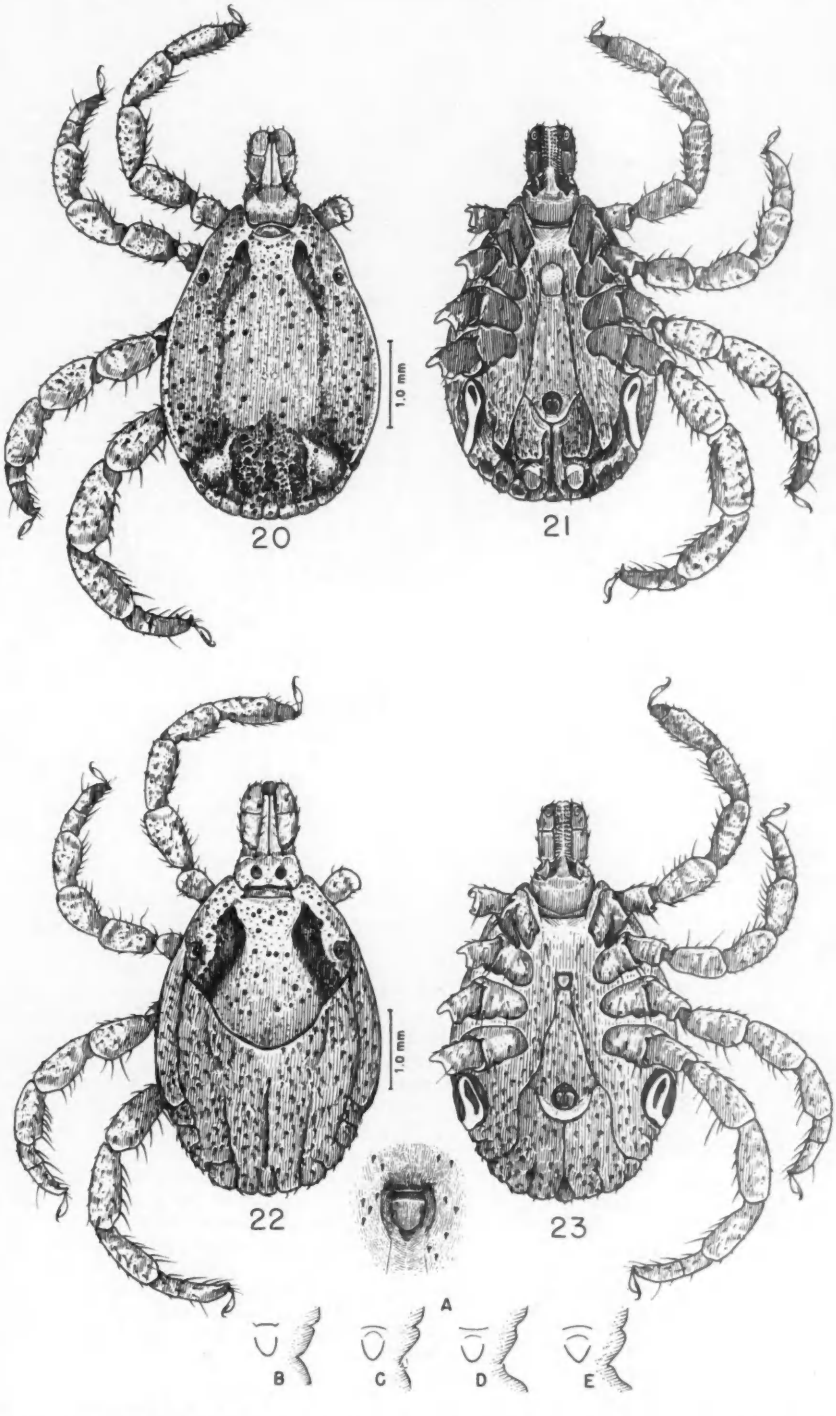
Female.—The scutum measures from 2.09 mm. to 2.61 mm. in length (or possibly more) and from 2.04 mm. to 2.42 mm. (or more) in width; average specimens are 2.33 mm. in length and 2.23 mm. in width. The scutum is darker, somewhat more heavily punctate, and with large punctations deeper than those of the subspecies *anatolicum*. The bulging genital apron is typically widely triangular in outline; it may also be circular or widely triangular. The legs are light brown, usually with faint reddish brown rings, and usually marbled when dry.

The type specimen.—Koch's type specimen was noted by Kratz (1940, p. 531) to be "a male from Egypt with a large depressed caudal field and incomplete pons over the white parma." It was described by Feldman-Muhsam (1954, p. 156) as follows: "The length of the scutum is ca. 4 mm., the width ca. 2.6 mm. The cervical grooves are long and superficial. The lateral grooves are very short. The parma is white. The third, fourth, and fifth festoons are fused. At the fused festoons starts a longitudinal elevation which extends anteriorly to the hinder part of the scutum. Between these elevations, the whole caudal field is strongly depressed. The depressed field is finely punctated. The outer margin of the anal plates is strongly convex laterally. The inner margin of the anal plates form an acute extension behind the anus." Illustrations after Feldman-Muhsam are reproduced herein (figures 19A, B).

Feldman-Muhsam's description and illustrations tally exactly with the critical diagnostic characters for identification of typical specimens of the subspecies *excavatum*. These features are length and width of the scutum, anterior fusion of paraparmal festoons, obscurity of posteromedian groove, absence of large punctations in caudal depression, elevated ridges beside caudal depression, length of cervical grooves, large size of subanal shields, and robustness and convex external margins of adanal shields.

COMPARISON OF *H. anatolicum excavatum* AND *H. franchinii*

Males of the apparently uncommon and geographically limited species *H. franchinii* Tonelli-Rondelli 1932(A), morphologically are superficially fairly similar to those of *H. anatolicum excavatum*, but their females are readily distinguishable and biological characteristics of each form are unique (see Hoogstraal and Kaiser,



FIGS. 20–23.—*H. lusitanicum* ♂ and ♀, dorsal and ventral, Portugal (Specimens presented by Dr. J. Tendeiro).

1958A, B). In an artificial key to males, these two forms might appear to be closely related; we believe, tentatively, that they are not closely related phylogenetically. The comparative characters below should easily differentiate these two forms.

H. franchinii	*H. anatolicum excavatum*
MALES	
Scutum round-oval average, 4.18 x 2.74 mm.	comparatively elongate-oval, 4.50 x 2.95 mm.
Cervical field smooth with few large punctations	less smooth, more punctate
Cervical grooves smooth, short; confined to anterior third of scutum	deeper, longer; usually extending beyond anterior third of scutum
Parma usually elongately triangular	broadly triangular or subrectangular
Paraparmal festoons not extending as pons	usually as pons
Second pair of festoons long	short, truncated by paramedian grooves
Caudal field triangular, with straight lateral margins	lateral margins irrgularly rounded
Spiracular plates with long, thin, tapering tail	tail moderately wide, slightly curved apically
Adanal shields with slight posteromedian indentation	lacking posteromedian indentation
Subanal shields small or frail	always strong
FEMALES	
Genital apron short, covering basal half of aperture	long, bulging over entire length of aperture
Scutum with broadly rounded posterior margin	more elongate and narrowly rounded posteriorly
Cervical field glossy, with few large punctations	more punctate
Cervical grooves shallow, smooth, faint posteriorly	deep, more punctate laterally, reach posterior margin
IMMATURE STAGE (BIOLOGY)	
Usually infest reptiles	usually infest small mammals

Hyalomma (Hyalomma) lusitanicum Koch

The Lusitanian *Hyalomma*

(Figures 20–23, 26)

Hyalomma lusitanicum Koch, 1844, p. 222, short descriptions of ♂ and ♀ from Portugal; type material not subsequently reported as seen and obviously, by this time, destroyed or mislabelled.

H. lusitanicum Koch; Koch, 1847, pp. 14, 36–38, Plate 3, Figs. 10 and 11.Both sexes redescribed and illustrated.

H. aegyptium lusitanicum Koch; Neumann, 1911, p. 51, new synonymy.

H. lusitanicum lusitanicum Koch; Kratz, 1940, pp. 527–528, fig. 8, diagnosis of both sexes, in part confused with other species from Algeria; no type specimen mentioned.

H. excavatum Koch; Delpy, 1949B, pp. 476 and 487, new synonymy, type specimen not seen.

H. excavatum Koch; Feldman-Muhsam, 1954, p. 159, synonymy; type specimen stated to be lost.

H. lusitanicum Koch; Tendeiro, 1956, pp. 397–406, figs. 21–22, redescription of both sexes, illustrations of ♂ dorsal surface and ♀ genital aperture, includes extensive bibliography and history of synonymy, geographic range limited to Portugal and Spain.

H. lusitanicum Koch; Tendeiro (in press), selection and deposition of neotype from Portugal, in British Museum (Natural History).

DISTRIBUTION AND HOSTS

Material examined.—Total 75 ♂♂, 52 ♀♀; others from Morocco are being reared in our laboratories. PORTUGAL. 19 ♂♂, 6 ♀♀, from cattle, sheep, and *Dama dama* (Linnaeus) (fallow deer), Portel and Alentejo; HH collection, gift of Dr. J. Tendeiro. CANARY ISLANDS. 3 ♂♂, 11 ♀♀, from cattle, G. W. Perez leg. 1916, Nuttall lot 3226 in BM(NH), 1 ♂, 2 ♀♀ in HH collection. MOROCCO. 31 ♂♂, 31 ♀♀, from European rabbits, *Oryctolagus cuniculus* (L.), Nefifik Forest near Casablanca, HH collection, gift of Dr. G. Blanc (see Blanc and Bruneau, 1956, as *H. excavatum*). ITALY. 21 ♂♂, 1 ♀, from cattle, sheep, and goats, Augusta (Siracusa), Catafini, and Agrigento, HH collection, gift of Professor O. Starkoff. FRANCE. 1 ♀, from man, Le Trayas.

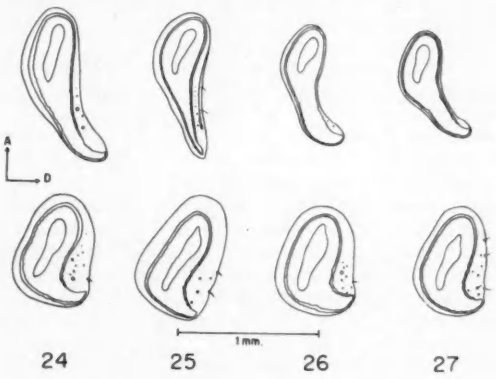
ITALY. *H. lusitanicum* is replaced by *H. a. anatolicum* in Sicily, Puglia, and Calabria, e.g. Sicily and southern Provinces of the mainland (Professor O. Starkoff, personal communication). SPAIN. Reported by Tendeiro (1956, p. 398), from *Cervus elaphus* subsp. (red deer); no locality. CANARY ISLANDS. Specimens from pigs have been received by Dr. J. Tendeiro (personal communication).

Summary.—The known range of *H. lusitanicum* is Italy (except Sicily, and southern Provinces of the mainland), southern France, Spain, Portugal, Morocco, and Canary Islands. Known hosts are cattle, sheep, goats, pigs, fallow deer, red deer, and European rabbits.

IDENTIFICATION

Male.—Small to medium size, reddish brown ticks with scutum averaging 3.70 mm. in length and 2.60 mm. in width (range 3.25 to 4.05 mm. in length and 2.40 to 2.80 mm. in width). Lateral grooves are extremely short or absent. The central field of the scutum has few large and scattered fine punctations that become more numerous and heavy laterally and in the cervical and scapular areas. Cervical grooves originate as deep pits and extend as smooth furrows to the scutal midlength. Posteromedian groove is faint and either does or does not reach the median festoon; paramedian grooves are short and indistinct, all three being more or less obscured by numerous punctations and sometimes rugosity of caudal depression. Festoons consist of one median and two other pairs; laterally festoons are fused and continuous with the raised ridge bordering the caudal depression. A unique, dirty white marbling (in preserved specimens) occurs in the scapular areas, between the cervical grooves, and may also be found on the basis capituli and ridges bordering the caudal depres-

sion. A parma is absent in all specimens. However, in single specimens from the Canaries and Italy it is possibly very faintly developed and Dr. Tendeiro (personal communication) has also recently received specimens from the Canaries with a parma questionably present. The spiracle has a thick, long tail. The adanal shields are robust, fairly short, rectangular, and mostly indented in the mid-posterior margin. The fairly large subanal shields lie directly posterior of them and are usually rounded posteriorly. The reddish brown legs are usually conspicuously and extensively marbled when dry.



FIGS. 24–27.—Spiracular plates of *H. anatolicum excavatum* (24), *H. franchinii* (25), *H. lusitanicum* (26), and *H. a. anatolicum* (27). Drawn from ticks, not from mounts. ♂♂, upper row. ♀♀, lower row.

Females.—The comparatively wide, short scutum in our specimens measures approximately 2.20 mm. in length and 2.00 in width; its reddish brown to dark brown color is extensively marbled when dry, as are the basis capituli and dorsal surfaces of the palpi. Punctations are comparable to those of the male. Cervical pits are very deep. Cervical grooves are deep, broad, extending to the posterolateral margin of the scutum, and usually with some large punctations and lateral rugosity. The genital apron, more or less widely shield like in outline, does not bulge in profile (thereby definitely establishing this as a species differing from *H. anatolicum* subspp.) but is gradually depressed posteriorly. The reddish legs, as in the male, are extensively marbled.

Original description.—Koch's original description, translated, is as follows:

"12. *H. lusitanicum*—Scattered punctations, wine-red, a small, round edge white. Legs rust-red sprinkled with brown-red, the border of the segment bright light yellow, likewise brown-red sprinkled. Length 1⅔″. Male."

"Just the same, the coarsely punctate thorax is ringed anteriorly in yellow; the wrinkled posterior area dark wine-red, on the sides dark yellowish. Length 1¾″. Female."

"Origin: Portugal."

From Koch's numerous references in the original description and in the 1847 redescription to contrasting coloration, and from the geographical origin of the material, there appears to be no doubt of the association of material today considered to be *H. lusitanicum* with that originally described under this name.

KEY TO *H. ANATOLICUM* GROUP

MALES

Lateral grooves absent or less than one third scutal length. Subanal shields situated directly posterior of adanal shields (except in greatly engorged individuals). Punctations few to moderately dense but never dense or regularly distributed over scutum, variable in size and depth. Cervical grooves extend for at least one-third length of scutum. Caudal area depressed between two more or less raised ridges; posteromedian groove distinct, narrow, confined to caudal depression. Small to moderately large ticks..... (GROUP CHARACTERISTICS)

1. Medium size ticks with lateral grooves absent or at most not even so long as caudal depression. Parma usually absent or indistinct. Scutum with numerous small punctations; large punctations of various depths usually more dense and deep laterally, on scapulae, and between cervical grooves; ridges beside caudal depression distinctly elevated; caudal area with numerous rather large, deep, contiguous punctations; posteromedian groove often containing punctations but usually distinct and bordered by two small ridges; paramedian grooves usually obscure. Adanal shields short, robust, rectangular. Spiracular plate with a thick, long tail. Leg segments often extensively marbled (when perfectly dry) dorsally and apically. Southwestern Europe, northwestern Africa **H. lusitanicum**

Small to moderately large ticks with above combination of characters varying. Lateral grooves usually approximately one-fourth of scutal length. Parma usually present and distinct. Scutum only exceptionally as punctate as above, usually smooth with few widely scattered large punctations and faint small punctations; caudal area usually with comparatively few large punctations and more numerous small punctations. Spiracular plate with thin, long tail (*H. anatolicum*, 2 forms)..... 2

2. Moderately large, tough, reddish brown to dark brown ticks, scutal length usually over 4.00 mm. Ridges beside caudal field distinctly elevated. Subanal shields heavily chitinized, never rudimentary. Legs light brown, marbled when dry.. **H. anatolicum excavatum**

Small, frail, pale ticks; scutal length up to 3.85 mm. pale to pale reddish brown. Ridges beside caudal field weakly elevated. Subanal shields weak, often rudimentary or absent. Legs yellowish or pale brown, never marbled when dry... **H. a. anatolicum**

FEMALES

Genital aperture either oval (shieldlike) and gradually depressed posteriorly or rounded or triangular (knoblike), short and bulging posteriorly. Scutum usually somewhat longer than wide, posterior margin comparatively narrowly rounded. Cervical grooves deep, broad, reaching posterior margin of scutum. Scutal punctations as anteriorly in males.....(GROUP CHARACTERISTICS)

1. Genital apron outline elongate, shieldlike; profile gradually depressed posteriorly. Cervical grooves broad, with some punctations and lateral rugosity. Scutal punctations as in male..... **H. lusitanicum**

   Genital apron small, outline short, triangular; profile knoblike, slightly bulging. Cervical grooves narrow, smooth, with few punctations. (*H. anatolicum*, 2 forms)..... 2

2. Scutum strongly chitinized, usually more than 2.00 mm. in length; color reddish brown to dark brown. Genital apron typically widely triangular; also may be circular or elongately triangular. Legs with faint reddish brown rings, usually marbled when dry..... **H. anatolicum excavatum**

   Scutum weakly chitinized, less than 2.00 mm. in length; color yellowish brown to brown. Genital apron circular or elongately triangular, widely triangular only when engorged. Legs very faintly striped with pale yellowish brown rings, never marbled..... **H. a. anatolicum**

DISCUSSION AND CONCLUSIONS

TAXONOMY

Hyalomma anatolicum Koch, 1844 (sensu Schulze) refers to *H. anatolicum excavatum* of the Pomerantzev school of Soviet workers while *H. excavatum* Koch, 1844 (sensu Delpy), as consistently and widely used by non-Soviet workers for at least a decade, refers to *H. anatolicum anatolicum* of the Pomerantzev school. This fact, which we have long suspected from review of Soviet literature, is now confirmed by comparison of Russian-identified specimens with those in the Schulze and in other collections.

After this circumstance was determined, our second problem concerned a critical questioning of the validity of the Pomerantzev opinion that the species *anatolicum* is composed of two subspecies, *anatolicum* and *excavatum*. We had already reported (Hoogstraal, 1956) a number of atypical specimens of *H. excavatum* and described and illustrated a closely related form, readily discernible as a separate morphological and biological taxon, as *H.* sp. number 2 near *excavatum*. Shortly after completion of the 1956 work, Mr. G. Kohls made available to us that part of the Schulze collection that we had not already seen. It immediately became evident from this material that Schulze's *anatolicum* was our *H.* sp. number 2 near *excavatum*. Thereupon, we spent several months restudying our *Hyalomma* collections. We were also privileged to examine the tremendous *Hyalomma* collections from Turkey belonging to the Rocky Mountain Laboratory. During this period, practically every one of our previously perplexing atypical specimens of "*H. excavatum*" was easily absorbed under *H. anatolicum* (sensu Schulze). Further, collation of biological data showed usually distinct biological characteristics of *H. excavatum* (sensu Delpy) and *H. anatolicum* (sensu Schulze). It was then obvious, even though non-Soviet workers from Delpy (1949A, B) to date had synonymized *anatolicum* under *excavatum*, that the two were related but distinct subspecies.

Our third problem was to determine whether Russian or non-Russian workers were correct in referring to *excavatum* as the larger of the two subspecies. Fortunately, Kratz (1940) had described some of the critical characters of the type specimen of *excavatum* and Feldman-Muhsam (1954) had nicely described, illustrated, and measured this specimen. The details of the type specimen of *H. excavatum* presented by these workers tally exactly with all material referrable to *H. anatolicum* (sensu Schulze); therefore it is obvious that non-Soviet workers had not only erroneously applied the name *excavatum* to the small subspecies, but had also incorrectly lumped the two forms [i.e. *excavatum* (sensu Delpy) and *anatolicum* (sensu Schulze)].

The fourth problem was what to do about the name *H. anatolicum* Koch owing to the loss of the type female and the sketchy original description, which is insufficient definitely to identify the species. Here, we were forced into an arbitrary decision, and selected a *neotype* from the same general area as the original specimen (i.e. eastern Turkey). In so doing, the bulk of significant published references to this species and its subspecies become taxonomically stabilized; these are in literature from the U.S.S.R., where *H. anatolicum* subspp. is widely spread and of considerable medical and veterinary importance. Pomerantzev was not only the only previous worker to interpret *H. excavatum* correctly and to recognize these two related subspecies, but he also discerned what Koch's *H. anatolicum* most probably was (herein arbitrarily established by a *neotype*).

A fifth, tangential, problem presented itself when studying variation in subanal shields and in other morphological characters of large series of *H. a. anatolicum* (sensu Pomerantzev). A certain number of abnormal individuals almost invariably develop when tremendous masses of this tick feed on a single animal, when the immature stages utilize exceptional hosts, or when the life cycle is spent entirely in a rigorous desert environment (Pomerantzev, 1950, p. 214; Hoogstraal, 1956, pp. 447–448, 520–523). These individual variants possess all the characters ascribed to the type specimen of *H. rhipicephaloides* Neumann, 1901, and to other material described under this name by Feldman-Muhsam (1957). We must, therefore, reiterate the common contention that *H. rhipicephaloides* Neumann, 1901, is a synonym of *H. a. anatolicum* Koch, 1844, and that the subgenus *Hyalommina* Schulze, 1919, erected for it, has no validity. Santos Dias (1956) independently arrived at the same conclusion and established the subgenus *Delpyiella* for the Indian species *H. hussaini* Sharif, 1928, which actually does lack subanal shields. Kohls, to whom we sent a representative sample from the lot illustrated herein, replied "Specimens such as these would appear to remove

any doubt about the status of *H. rhipicephaloides*." Similar abnormalities in other species of *Hyalomma* have also been named indiscriminately.

After these data and conclusions were set down, the preliminary manuscript was submitted to a number of distinguished colleagues with special interest in African-Asiatic ticks or in problems of zoological nomenclature. Various suggestions made by them have been incorporated into the report. Professor Serdyukova replied by calling attention to the current Soviet opinion, expressed by Pervomaisky (1954). As a result, we delayed submitting this report for some eight months during which we intensified and expanded our rearing experiments with both subspecies and with *H. lusitanicum*. The results, which amply confirm our thesis, will be presented in a subsequent section of this series.

BIOLOGY

Data referring to seasonal activities and immature-stage host-predilections of the two subspecies of *H. anatolicum* in Egypt confirm the morphological findings and definitely establish each as a separate, biologically and morphologically distinct, form. The geographic range of each is somewhat different and the ecological situations in which each occurs may, in some instances, differ dramatically. Once these two subspecies are better understood, additional biological criteria undoubtedly will be revealed.

Both forms have a wide, almost equal, geographic range, but both are replaced by *H. lusitanicum* in southwestern Europe. In Russia, both forms occur in Turkmen S.S.R., southern Kazakh S.S.R., and Tadzhik S.S.R., but only *anatolicum* also ranges into Daghestan, southern and eastern Transcaucasia, and Uzbek S.S.R. (Pomerantzev, 1950). Significantly, the subspecies *excavatum* does not breed in the cultivated Nile Valley and Delta where the subspecies *anatolicum* is ubiquitous. Furthermore, representatives of the subspecies *excavatum* are totally absent in our extensive collections from eastern Saudi Arabia, Iraq, and India, where the subspecies *anatolicum* is well represented. Present evidence suggests that *excavatum* is rare or possibly absent on the high Anatolian steppes and in the mountains of Kurdistan in eastern Turkey; the subspecies *anatolicum* is common in these areas.

The geographic distribution of the previously poorly known *H. anatolicum excavatum* is now established as scattered localities in a belt from Spanish Sahara (Rio de Oro) on the Atlantic Coast of North America across North Africa to Palestine, southwards on both coasts of the Red Sea into Yemen (southwestern Arabia), and into the Sudan, Eritrea, and French Somaliland (with possibly a non-established population once having been introduced into the mountains of Kenya). Northwards and eastwards it occurs in Crete, Greece, and associated islands, parts of Turkey, Turkmen S.S.R., southern Kazakh S.S.R., Tadzhik S.S.R., and Iran.

The geographic range of *H. a. anatolicum* is confirmed (as previously reported by Hoogstraal, 1956, for "*H. excavatum*", with the exception that it is replaced by *H. lusitanicum* in southwestern Europe) as common through all of northern Africa; it also ranges throughout southeastern Europe (southern Italy and Sicily eastwards), the Near and Middle East, Asia Minor, and southern Russia into India.

Ecologically, both forms are largely or entirely restricted to steppe lands, semidesert areas, and oases. While populations of each are usually separate and distinct on any homogeneous herd of domestic animals, a small proportion of interbreeding does occur in certain areas (see below). The subspecies *anatolicum* is definitely much more uniformly distributed than *excavatum* and generally consists of larger populations. In Egypt, as already stated, we find both forms on camels and cattle in desert and semidesert areas, but the subspecies *excavatum* never occurs on domestic animals restricted to the cultivated, nondesert Nile Valley and Delta, where the subspecies *anatolicum* is common.

Immature stages of the subspecies *anatolicum* almost without exception parasitize only hares and larger domestic animals while immature stages of the subspecies *excavatum* parasitize only smaller animals such as insectivores, rodents, and hares. Adults of the subspecies *excavatum* are considerably more common on camels in the deserts of Egypt and Libya than those of its related subspecies.

The subspecies *excavatum* breeds (mates) on its hosts in Egypt during all seasons of the year and especially during the cooler months when most members of local populations of the subspecies *anatolicum* are dormant, hiding away in cracks and crevices as either nymphs or adults.

It is noteworthy that *H. a. anatolicum* is widely distributed and studied in Russia but that the life cycle and biology of *H. anatolicum excavatum* remain unreported by Soviet workers. Both forms may undergo either a two-host or a three-host type or life cycle on the same experimental animals. Factors influencing this developmental variation, common in some *Hyalomma* species and apparently absent in others, remain to be discovered. The life cycle of the subspecies *excavatum* under experimental conditions is reported above, apparently for the first time.

Consideration of *anatolicum* and *excavatum* presently as allopatric (i.e., geographically isolated) subspecies is based on the following facts. (1) The geographical range of the two is similar but not equal, *excavatum* frequently being absent in large areas where *anatolicum* is common (i.e., Upper Egypt, eastern Saudi Arabia, Iraq, India, Daghestan, Uzbek S.S.R., etc.). (2) Where popu-

lations of the two forms meet, they interbreed in the usually fairly wide zone of contact. The incidence of such hybridization, as demonstrated by large samples (over 1,000 males) from several areas, varies locally from 2 percent to somewhat less than 20 percent. We believe that this higher rate is due entirely to one artificial factor, large herds of widely-traveling domestic camels and cattle. Primitively, these two forms probably arose as a result of ecological isolation. After centuries of transport on widely ranging domestic animals, some populations show some degree of intergradation. Nowhere in their extensive range are we aware that these forms violate or even closely approach the upper limit of the "75 percent rule" for designation of subspecies (see Mayr, Linsley, and Usinger, 1953). However, the extremely variable results obtained by Pervomaisky (1954) suggest that he has encountered one or more populations[2] where hybridization is rather more common than among most African-Asiatic populations.

ACKNOWLEDGMENTS

We are grateful to Mr. Glen M. Kohls of the Rocky Mountain Laboratory for the privilege of studying material in the Schulze collection and considerable numbers of specimens from Turkey. To Mr. E. Browning and Dr. G. Owen Evans we also owe thanks for the privilege of studying large collections of the British Museum (Natural History). Dr. J. Tendeiro, Professor O. Starkoff, and Dr. G. Blanc also kindly provided important specimens and data for this report.

In consideration of the rather delicate taxonomic considerations surrounding the present study, we have referred the manuscript to several specialists whose comments are much appreciated; these are Mr. G. Kohls and Dr. C. B. Philip (Hamilton), Professor G. V. Serdyukova (Leningrad), Dr. C. Sabrosky (Washington, D. C.), Professor J. Belkin (Los Angeles), Dr. J. Tendeiro (Lisbon), Professor O. Starkoff (Rome), Dr. G. Theiler (Onderstepoort), and Dr. P. Johnson (Washington, D. C.).

Mr. Sobhy Gaber has given invaluable assistance in the rearing experiments. The illustrations are the work of Mr. R. Strekalovsky.

[2]Dr. R. A. Ward, who read this manuscript after it was submitted for publication, writes ". . . the only conclusion that I can draw is that *H. anatolicum* and *H. excavatum* are distinct species. Your taxonomic and biological data all tend to support this contention. The only criterion for subspeciation indicated in your paper is in respect to areas of hybridization. And these I would interpret [as] areas of introgressive hybridization . . . where gene flow has occurred or is now occurring between two different species. . . . Your material provides the first case of introgression in ticks and should be designated as such."

Dr. Ward's contention may be entirely correct, and we hope either to prove it or disprove it by continued rearing experiments. Owing to the length of the tick life cycle, 2 or 3 years of effort will be required for this purpose. At the present time, the fact that two taxonomically differing forms do occur in nature is important for the epidemiologist to know; the exact taxonomic level can be determined when more details become available.

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THE INFLUENCE OF MOONLIGHT ON LIGHT-TRAP CATCHES OF MOSQUITOES[1]

MAURICE W. PROVOST[2]

ABSTRACT

Light-trap catches of mosquitoes representing seven genera were shown to average six times greater near new moon than near full moon. Nonattractant air sampling revealed no such lunar periodicity. The light-trap lunar periodicity resembles that reported for noctuid moths and probably reflects merely the cycle of contrast between light and background illumination as the moon passes through its phases. The moon-determined night illumination pattern is superimposed on night activity patterns peculiar to mosquitoes by species and sex.

The New Jersey light trap (Headlee 1932; Mulhern 1942) was developed specifically for mosquito sampling and has been extensively used throughout the world in both mosquito control and research. Its collections are so readily affected by variable factors residing in the trap itself, in the weather, in the environment generally, and especially in the mosquitoes, that they are never strictly proportional to the mosquito population. It follows then that the value of light-trap collections is proportional to what is known of the trap's abilities, limitations and eccentricities. Of the many environmental factors which affect the size of light-trap collections one of the most important is moon phase. Yet this effect is so easily swamped and masked by others that most trap operators seldom detect it. It is therefore necessary at once to emphasize that the moon-phase effect, in spite of its great magnitude, can be exposed and analysed only on the basis of a very large mass of operational data gathered over many months and preferably years. This is equally necessary in trying to establish whether the moon-phase effect is a matter of mechanical efficiency or a reflection of altered behavior in the insects, a problem this paper will attempt to elucidate.

In 1936 C. B. Williams, of the Rothamsted Experimental Station (England), published a very searching analysis of the moonlight influence on activity in nocturnal insects, particularly noctuid moths. With the Rothamsted light trap (Williams 1935), he demonstrated a ratio of noctuid captures between new and full moon of 3:1 on clear nights and 2:1 on cloudy nights. He found similar but less pronounced periodicities in other insect groups and none in some, and concluded that the moon effect was greatest in insects having their maximum activity at midnight and least in those flying chiefly at dusk or dawn. There remained unexplainable features, however, and he surmised that the moon effect "is probably a physiological effect on the activity of the insects and not merely due to reduction in the efficiency of the light trap when the moon is shining" (Williams 1936, p. 389). He later (Williams 1940) refined his analysis of asymmetries in the moon effect and correlated these with asymmetries in the times of rising and setting of the moon. Again at Rothamsted in 1940 a suction trap showed lunar periodicities in captures of Diptera (Williams and Singh 1951) and since light attraction was not involved it was concluded "that the moonlight must have a definite effect on nocturnal insects, and that the low catches in a light trap at full moon are not merely due to a physical reduction of the efficiency of the trap" (p. 853). However, later and more exhaustive experiments with suction traps failed to duplicate the 1950 results, forcing the conclusion that:

[1]Contribution No. 65, Florida State Board of Health, Entomological Research Center, Vero Beach, aided by grant E-1492, National Institutes of Health, U. S. Public Health Service. Accepted for publication September 18, 1958.

[2]Director, Entomological Research Center.

"We are, therefore, still without any evidence of an effect of moonlight on the activity or distribution of night-flying insects, except in the case of some aquatic species, where the influence appears to be on the emergence from the water and so on the size of the adult winged population" (Williams et al 1956, p. 143).

The moon effect on light trap captures of mosquitoes was noted early. In reporting studies with the New Jersey light trap at Zellwood, Florida, in 1932, Bradley and McNeel (1935) stated: "A bright moon over any considerable period also appeared to be unfavorable, the trap accumulating the largest numbers on still, dark nights" (p. 783). The chief mosquitoes involved were *Mansonia perturbans* (Walker) and *Anopheles crucians* Wiedemann. Horsfall (1943) in Arkansas noted a very pronounced correlation of *Anopheles quadrimaculatus* Say light-trap catches with lunar cycles, numbers rising greatly at the new moon and falling sharply at the full of the moon. His explanation was: "The darker the night, the greater the area over which the light trap exerts its attractiveness, and consequently the greater the numbers of mosquitoes attracted, other things being equal" (p. 44). Pratt (1948) obtained similar results in Puerto Rico with *Anopheles albimanus* Wiedemann in New Jersey light traps and found no moon effect on parallel catches in horse- or calf- baited stable traps. He had previously shown (Pratt 1944) that New Jersey light traps attracted this species in proportion to the wattage of the bulb used, so he concluded (Pratt 1948, p. 219) that the numbers of *A. albimanus* collected in light traps varied "with the relative intensity of the light given out by the light trap—whether due to the wattage of the bulb employed in the trap or due to the relative illumination given out by a bulb of fixed wattage competing with moonlight whose intensity fluctuates cyclically every four weeks."

It appears then that British and American investigators working unbeknown to one another, one group on agricultural insects and the other on public health insects, arrived essentially at the same conclusion. Light trap captures of night-flying insects varied inversely with the intensity and duration of moonlight, probably because moonlight diminished the contrast between background and the light emitted by the trap. The data herewith presented corroborate this explanation and extend its application.

GAINESVILLE EXPERIMENT—1948

From July 30 to November 1, 1948, three New Jersey light traps were operated nightly at the edge of a woodland near Payne's Prairie, south of Gainesville. Although the total trap run extended over only three lunar cycles, there was a sufficient number of collections to yield a moon periodicity in captures of some of the continuously producing mosquitoes species (fig. 1).

The results for *A. quadrimaculatus*, *A. crucians*, and *M. perturbans* revealed captures near new moon to be regularly larger than those at full moon, the ratios for the two sexes of these species (table 1) varying only from 6:1 to 9½:1. These ratios are based on too few lunar cycles to be definitive by themselves.

Table 1.—Comparison of average (5-day moving) mosquito collections in New Jersey light traps at peak of captures near new moon and at low point near full moon.

Species and Sex	Highest Point		Lowest Point		High/Low Point
	Moon Age	Average Collection	Moon Age	Average Collection	
A. Payne's Prairie, July 30—November 1, 1948					
♀ *A. quadrimaculatus*	0	6.09	14	1.02	5.96
♂ *A. quadrimaculatus*	28	2.81	14	0.40	7.03
♀ *A. crucians*	0	36.44	15	5.43	6.71
♂ *A. crucians*	0	6.04	15	0.67	9.01
♀ *M. perturbans*	0	9.33	14	1.49	6.26
♂ *M. perturbans*	4	4.05	13	0.43	9.41
Average	1	——	14	——	7.40
B. Leesburg, April 1—October 31, 1949					
♀ *A. quadrimaculatus*	5	16.0	15	4.9	3.26
♀ *A. crucians*	2	20.9	14	5.3	3.95
♂ *A. crucians*	28	4.1	13	0.5	8.20
♀ *A. walkeri*	2	22.8	15	6.2	3.67
♀ *M. perturbans*	27	134.0	14	14.0	9.57
♂ *M. perturbans*	28	5.8	14	1.1	5.27
♀ *M. indubitans*	3	271.0	11	129.0	2.10
♂ *M. indubitans*	20–6	39.0	11	11.0	3.54
♀ *C.* (*Culex*) spp.	2	77.2	14	14.3	5.84
Average	1	——	14	——	5.49

LEESBURG EXPERIMENT—1949

From April 1 to October 31, 1949, two New Jersey light traps were operated nightly on the outskirts of Leesburg as checks on the control work being done within the city limits (Provost 1952). When the collections are arranged by age of moon in days, the 7½ lunar cycles average out as clearly discernible lunar periodicities (fig. 2) for several species of continuously producing mosquitoes: *Anopheles quadrimaculatus*, *A. crucians*, *A. walkeri* Theobald, *Mansonia perturbans*, *M. indubitans* Dyar and Shannon, and *Culex* (*Culex*) spp. which were mainly *C. nigripalpus* Theobald. The disparity between new moon and full moon catches (table 1) was not quite as great as noted the year previous at Gainesville.

Sex differences in the lunar periodicity curves for the Leesburg collections (fig. 3) are interesting.

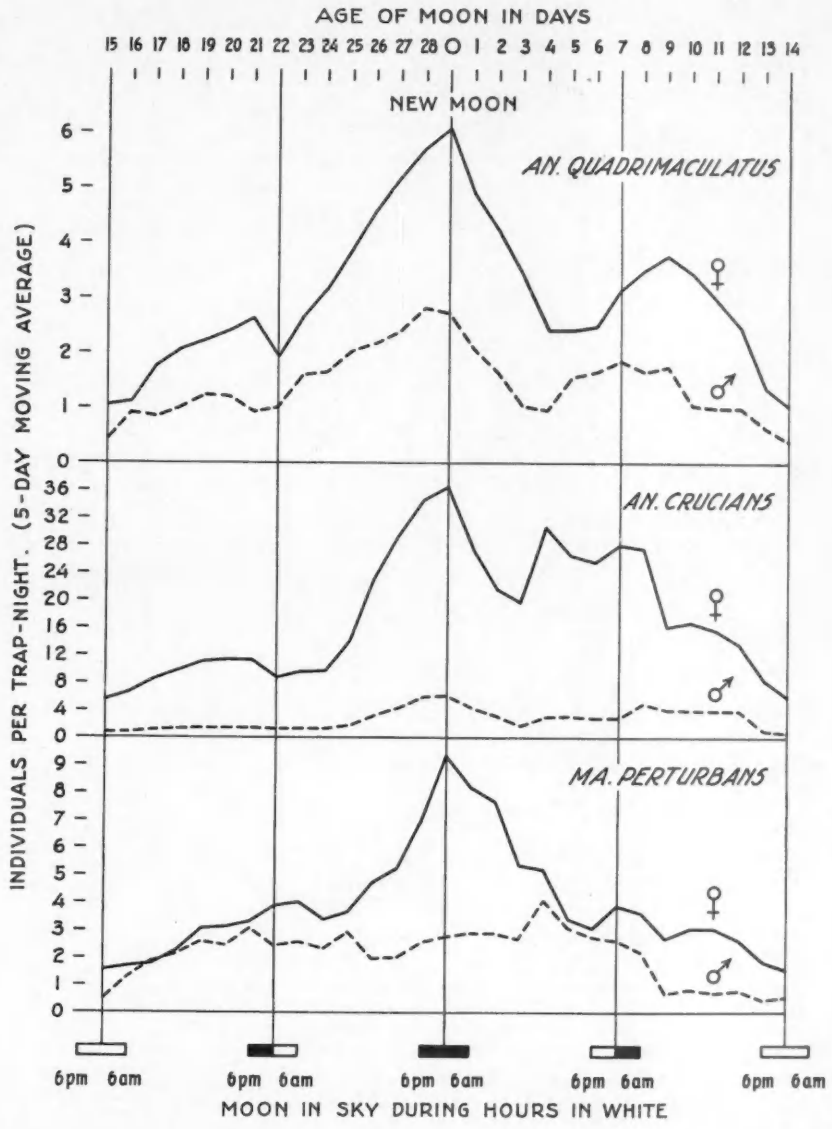
AGE OF MOON IN DAYS
15 16 17 18 19 20 21 22 23 24 25 26 27 28 O 1 2 3 4 5 6 7 8 9 10 11 12 13 14
NEW MOON
AN. QUADRIMACULATUS
AN. CRUCIANS
MA. PERTURBANS
♀
♂
INDIVIDUALS PER TRAP-NIGHT. (5-DAY MOVING AVERAGE)
6pm 6am
MOON IN SKY DURING HOURS IN WHITE

FIG. 1.—Light-trap catches of mosquitoes averaged according to moon age. Three traps operating nightly, July 30 to November 1, 1948, Payne's Prairie near Gainesville, Florida.

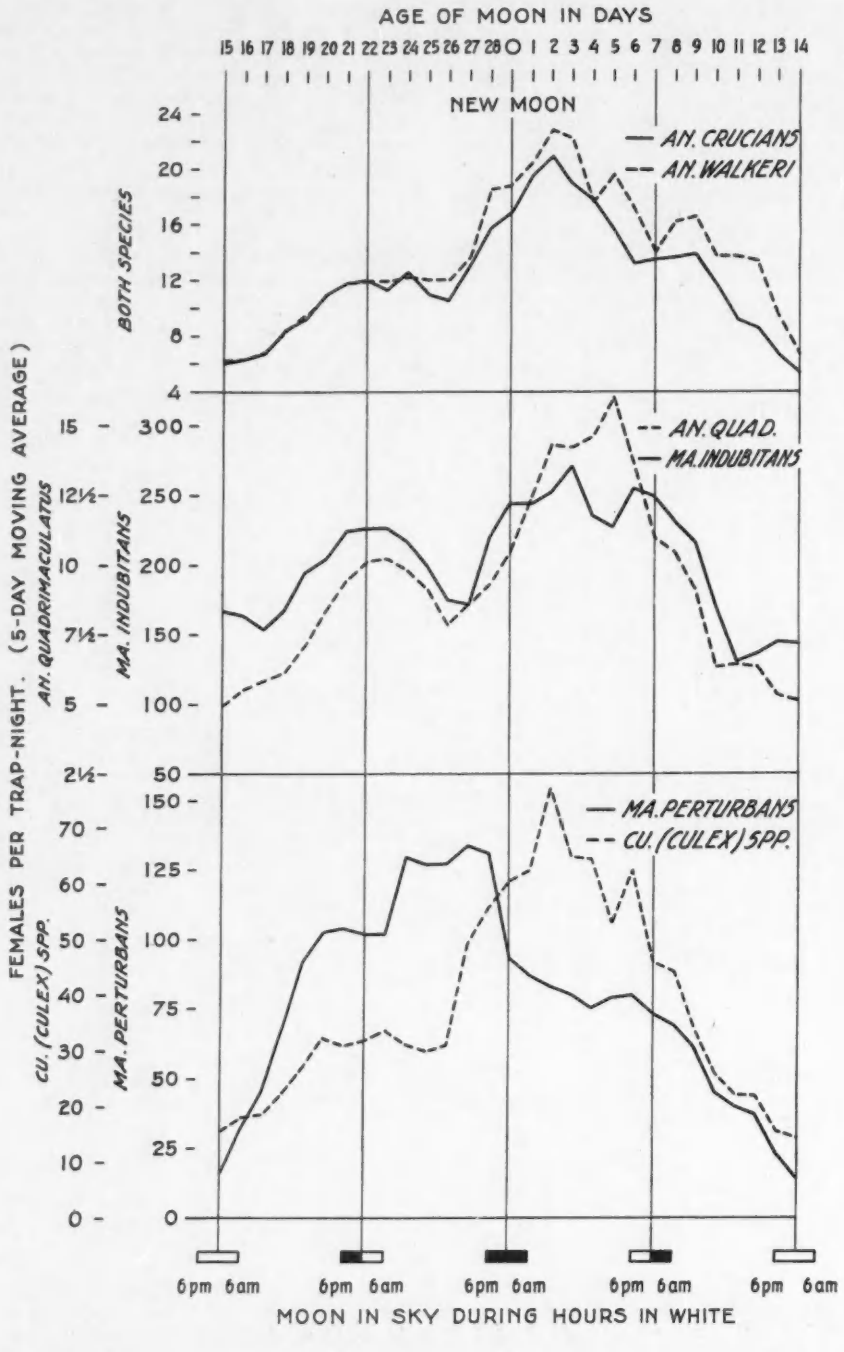
AGE OF MOON IN DAYS
15 16 17 18 19 20 21 22 23 24 25 26 27 28 O 1 2 3 4 5 6 7 8 9 10 11 12 13 14
NEW MOON
FEMALES PER TRAP-NIGHT. (5-DAY MOVING AVERAGE)
BOTH SPECIES
AN. QUADRIMACULATUS
MA. INDUBITANS
CU. (CULEX) SPP.
MA. PERTURBANS
AN. CRUCIANS
AN. WALKERI
AN. QUAD.
MA. INDUBITANS
MA. PERTURBANS
CU. (CULEX) SPP.
6pm 6am 6pm 6am 6pm 6am 6pm 6am 6pm 6am
MOON IN SKY DURING HOURS IN WHITE

FIG. 2.—Light-trap catches of mosquitoes averaged according to moon age. Two traps operating nightly, April 1 to October 31, 1949, outside Leesburg, Florida.

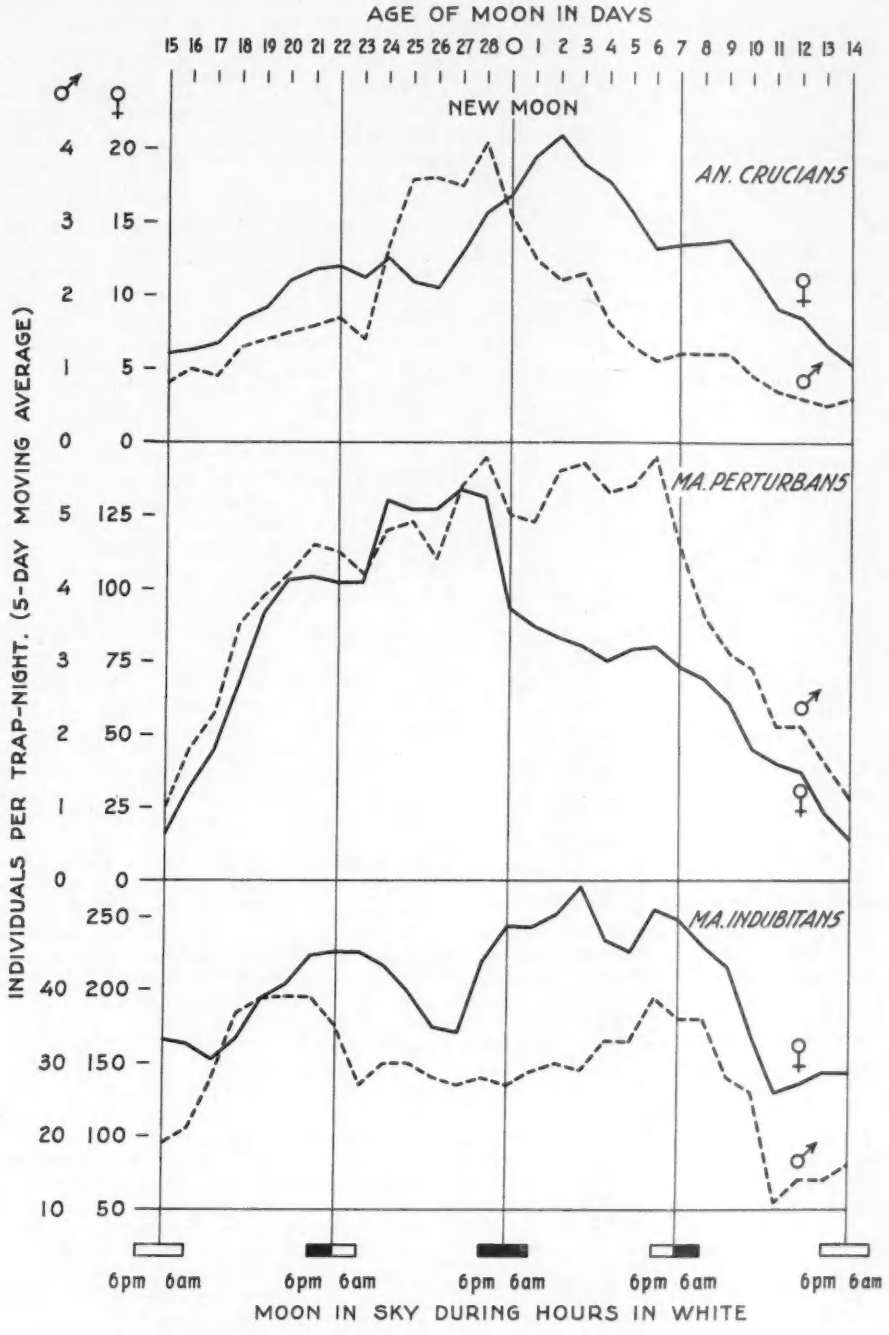
AGE OF MOON IN DAYS
15 16 17 18 19 20 21 22 23 24 25 26 27 28 O 1 2 3 4 5 6 7 8 9 10 11 12 13 14
NEW MOON
AN. CRUCIANS
MA. PERTURBANS
MA. INDUBITANS
INDIVIDUALS PER TRAP-NIGHT. (5-DAY MOVING AVERAGE)
6pm 6am
MOON IN SKY DURING HOURS IN WHITE

FIG. 3.—Leesburg (cf. Fig. 2) light-trap lunar periodicities, showing sexual differences.

It is tempting to theorize on differences between species and sexes in activity cycles at night, but these curves may be artifacts in their details. It does appear very likely, however, that the effect of the various moon phases on light trap catches is influenced by the time of night when the particular mosquitoes are most active, as shown for noctuid moths by Williams (1936).

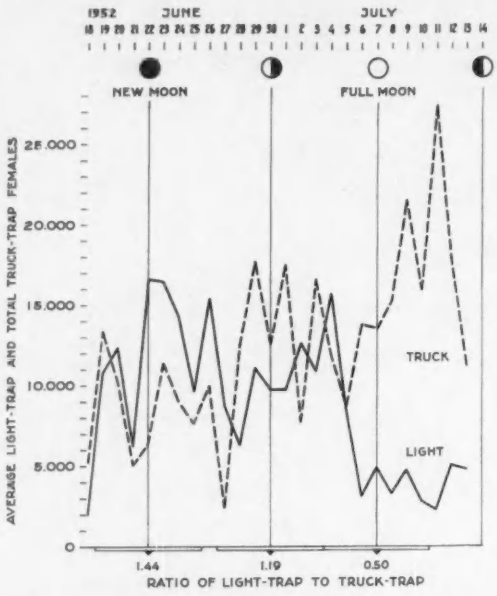

FIG. 4.—Comparison of nightly collections in truck-mounted funnel trap, three runs of an 18-mile route per night, with average collections of six light traps along route. Sanibel, Florida.

SANIBEL ISLAND EXPERIMENT—1952

In June and July 1952 Sanibel Island, off the southwest coast of Florida, was the scene of a marking-release-recapture experiment with *Aedes taeniorhynchus* (Wiedemann) to elucidate mosquito dispersal (Provost 1957). Several sampling devices were operated nightly for a month for recovery purposes; among these were New Jersey light traps and truck-mounted funnel traps. Since three large broods of wild or unmarked *A. taeniorhynchus* emerged during the experiment, centering on June 17, June 26, and July 9, there was a continuing and vast population of this mosquito on the wing. From June 17 to July 13, the truck traps made an 18-mile circuit three times a night, starting at 20^h, 23^h, and 04^h. Along the route were six light traps. Considering females only, it is seen (fig. 4) that the ratio of light trap to truck trap collection diminished from a 7-day average of 1.44 at new moon to an average of 0.50 at full moon. The depressing effect of full moon was great enough in this instance to prevent the light-trap record from reflecting an actual increase in the mosquito population.

VERO BEACH EXPERIMENTS—1955–56

From September 1955 to October 1956 a New Jersey light trap was operated at the edge of the salt marsh at Vero Beach ("Beach" trap) and a rotating-net trap was operated simultaneously within 100 feet, but where the light from the light trap did not reach. The rotor trap, sampling 9600 cubic feet of air per minute, consistently captured more mosquitoes than the light trap with a 60-watt frosted bulb.

The predominant species were *Aedes taeniorhynchus* and *A. sollicitans* (Walker), the two common salt-marsh mosquitoes, and *Deinocerites cancer* Theobald, the crab-hole mosquito (fig. 5). Since the two *Aedes* are discontinuous breeders, the thirteen lunar cycles were still not sufficient to cancel out the overriding influence of production (or emergence) on the trap catches. In *Deinocerites*, however, where production is more continuous, the light trap curve shows a definite moon effect whereas the rotor trap curve does not. This seems quite definitely to contradict any hypothesis that the moon effect is directly on the insect's activity.

ANALYSIS BY VARIATION FROM MEAN

When catches of animals in traps vary as considerably from day to day as mosquitoes do in light traps, arithemetical means are always in danger of being drastically affected by individual abnormally high or low collections. In his noctuid study, Williams (1936) circumvented this hazard by resorting to logarithmic expressions. For purposes of the present study, the same can be accomplished by using percentage of positive deviation from means averaged out for each day of the lunar cycle, the curve being further smoothed out with a 5-day moving average, as did Williams. This can be done with data at hand from the Leesburg 1949 trappings and from the Vero Beach 1955–56 trappings at the Beach (see above) and at the Laboratory ("E.R.C." trap) where a 60-watt New Jersey light trap also operated nightly. The results (fig. 6) are a convincing array of moon effect curves which peak near new moon in all cases except the known discontinuous breeders (*Aedes* spp.) or species breeding discontinuously during the study periods (*A. crucians* and *Uranotaenia sapphirina* (Osten Sacken) at E. R. C.). When the height of the peak in each curve is divided by that of the low point (table 2), the ratio of female captures at new moon to captures at full moon varies from 2:1 in *Mansonia indubitans* at Leesburg to 14:1 in *Deinocerites cancer* at the Beach trap. The average for all eight species concerned is about 6.3:1, comparing well with female averages differently computed from data in table 1 (6.3:1 and 4.7:1).

AEDES AND PSOROPHORA

As the data from Vero Beach will demonstrate, it is not possible with discontinuous breeders to show a moon effect on light-trap catches from analysis of a few consecutive lunar cycles, as has so far been done. It is possible, nevertheless, to demonstrate a moon effect even in such mosquito species.

The Florida State Board of Health has had a large number of New Jersey light traps (60 to 110 per year) operating on a fixed schedule for many years. These traps are distributed throughout the state and operate continuously on a fixed semi-weekly schedule—every Tuesday and Friday night. From a 10-year record of such trapping, 1947 to 1956, has been extracted all collections of

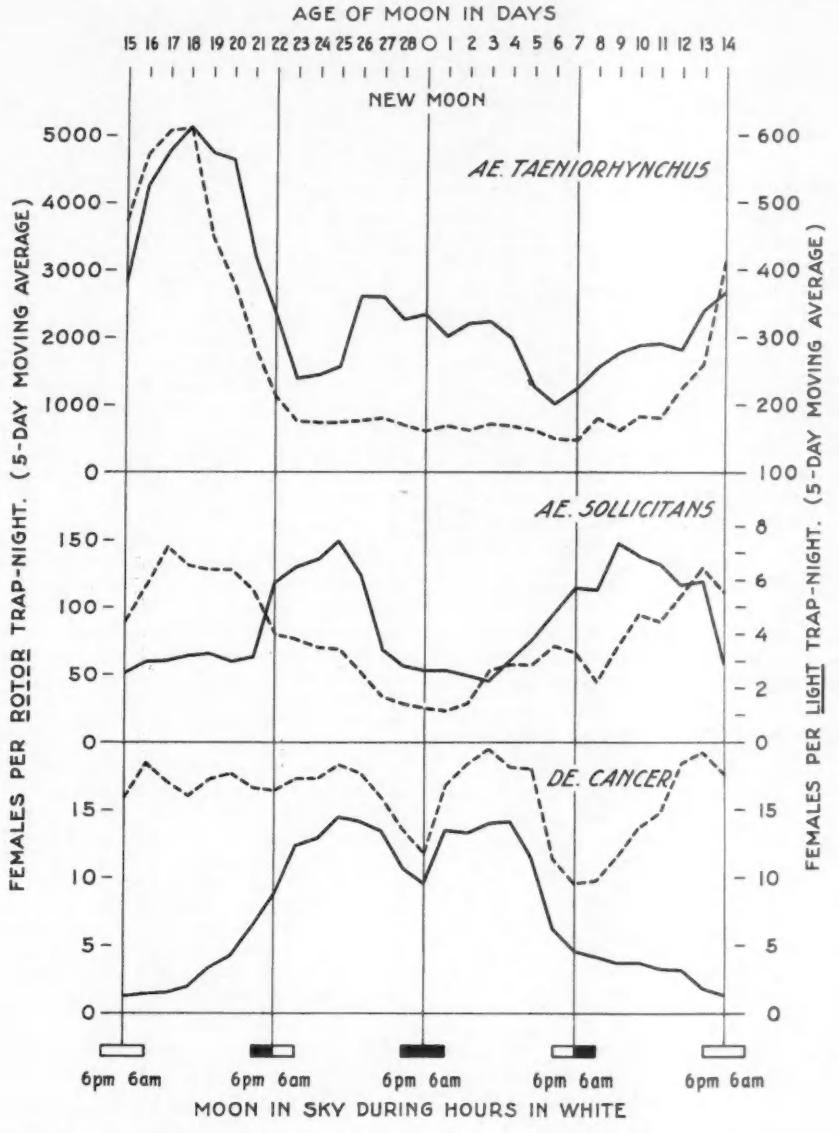

FIG. 5.—Catches in a light trap and a nearby rotating net trap averaged according to moon age. September 1955 to October 1956, at edge of salt marsh near Vero Beach, Florida.

Table 2.—Comparison of average (5-day moving) mosquito collections exceeding mean in New Jersey light traps at peak of captures near new moon and at low point near full moon; females only. Leesburg (1949) and Vero Beach (1955–1956) trappings.

Location	Species	Percent Greater than Mean		High/Low Point
		High Point	Low Point	
Leesburg	*A. quadrimaculatus*	48	15	3.20
	A. walkeri	47	17	2.77
	A. crucians	62	11	5.63
	M. perturbans	36	4	9.00
	M. indubitans	49	23	2.13
	C. (Culex) spp.	41	11	3.73
E. R. C.	*A. crucians*	34	17	* 2.00
	A. atropos	24	5	4.80
	U. lowii	28	3	9.32
	U. sapphirina	22	7	* 3.14
	A. taeniorhynchus	30	17	* 1.76
	A. sollicitans	40	15	* 2.67
	D. cancer	49	6	8.17
Beach	*A. taeniorhynchus*	34	19	* 1.79
	A. sollicitans	27	13	* 2.08
	D. cancer	58	4	14.50
Average, exclusive of those not breeding continuously (*)		—	—	6.34

female *Aedes taeniorhynchus* exceeding 10,000 in one night, and a random (with respect to moon age) sample of 191 large collections resulted. From the same record there were culled 204 collections of female *Aedes sollicitans* exceeding 250, and 162 collections of female *Psorophora confinnis* (Lynch Arribalzaga) exceeding 500. The moon age at each of these 557 collections was then determined and the data plotted in fig. 7. A very clear lunar periodicity is evident for all three species—in all cases with least captures on or close to the full moon.

On the basis of the above analysis the ratio of high to low points (as in tables 1 and 2), or the ratio of captures near new moon to those near full moon is 8.9:1 for *Aedes taeniorhynchus*, 3.0:1 for *Aedes sollicitans*, and 2.4:1 for *Psorophora confinnis*. The average for these three flood-water mosquitoes is therefore about 5:1, or well within the range found among the continuously-breeding species of *Anopheles*, *Culex*, *Mansonia*, *Uranotaenia*, and *Deinocerites*.

Table 3.—Percent collections of females above means, average of seven consecutive nights centering on new moon and full moon compared.

Test	Species	% Collections above Mean		
		New Moon	Full Moon	N/F
Leesburg 1949	*A. quadrimaculatus*	38.6	17.3	2.22
	walkeri	42.7	22.7	1.88
	crucians	42.7	16.7	2.56
	M. perturbans	27.6	7.1	3.89
	indubitans	45.1	26.9	1.67
	C. (Culex) spp.	34.7	13.1	2.65
E. R. C.	*A. atropos*	18.1	7.0	2.59
	U. lowii	18.3	5.1	3.58
	D. cancer	45.7	8.0	5.70
Beach	*D. cancer*	43.9	6.9	6.35
	Average			3.31

DISCUSSION

It has been shown that a variety of mosquito species representing seven genera are captured in light traps according to a lunar periodicity and that everything else being equal the traps will yield approximately six times as many mosquitoes at new moon as at full moon. Since emergence of adults is never really constant, even in the most continuous breeders, and since many other environmental factors affect the operation of light traps, the ratio 6:1 is not fixed at all but will always be a rough approximation arrived at only after averaging out the captures of many moon cycles. This ratio is nevertheless twice that found by Williams for noctuid moths on clear nights. This is apparently attributable to the fact that his comparisons are between several days intervals at new and full moon respectively. If the data given above are arranged so that percent of collections exceeding the means is compared for seven consecutive nights centering on new moon and on full moon (table 3), the ratios range from 1.67 to 6.35 to one and average out at 3.31:1.00, very close to the findings of Williams and his co-workers.

If the moon effect on light trap captures were mediated solely through physiological or behavioristic reactions to night light intensities, the difference among insect species and groups would

almost certainly be very great. The remarkable similarity of figures between such dissimilar insects as noctuid moths and mosquitoes, and the limited range of differences among mosquito genera and species (cf. tables 2 and 3), suggest rather strongly that a universal phenomenon is involved. This appears to be the relative intensity of background illumination at new moon and full moon. Thus the lunar periodicity in light-trap captures of any night flying insect may be the result of a purely physical cycle in the attractant efficiency of the light trap.

It is noticeable in most curves depicting lunar periodicities (figs. 2, 3, 5, 6) that peaks seldom

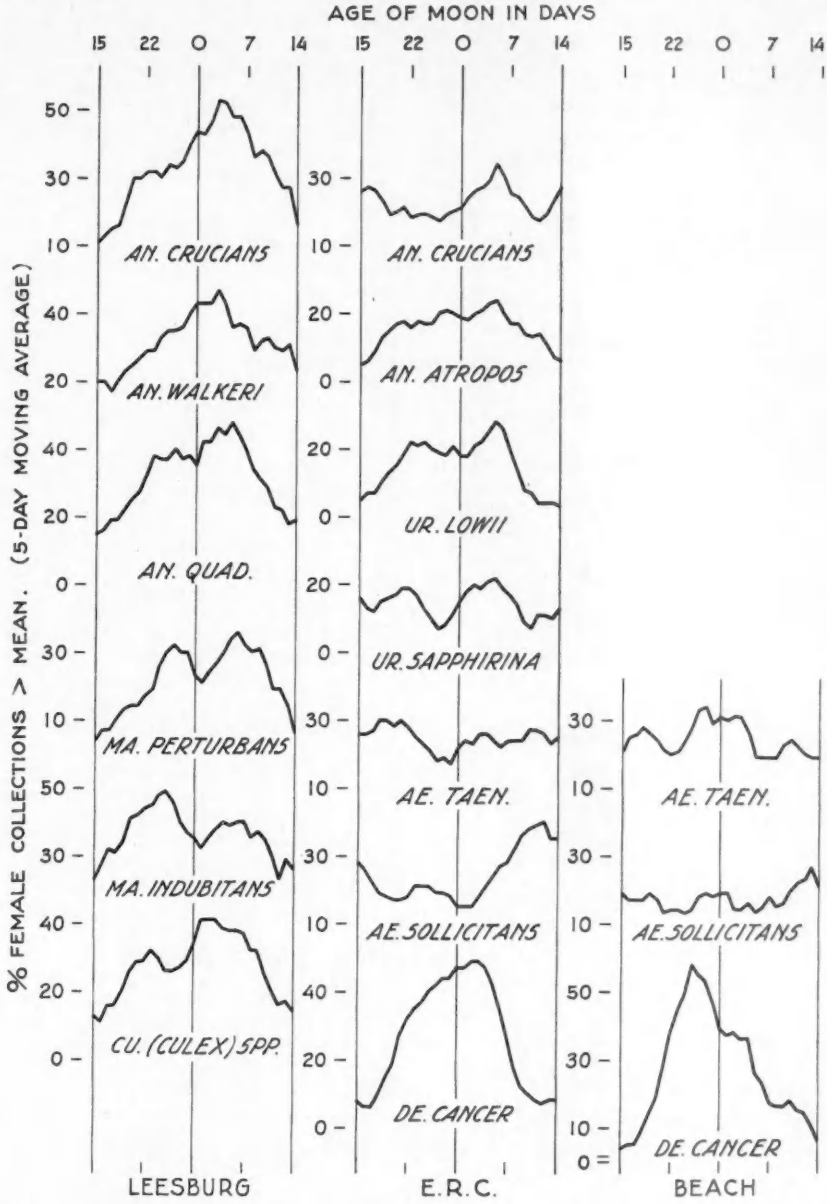

FIG. 6.—Lunar periodicity curves for Leesburg, Vero Beach, and Entomological Research Center (E.R.C.) light traps, expressed as percent of collections exceeding mean for lunar period.

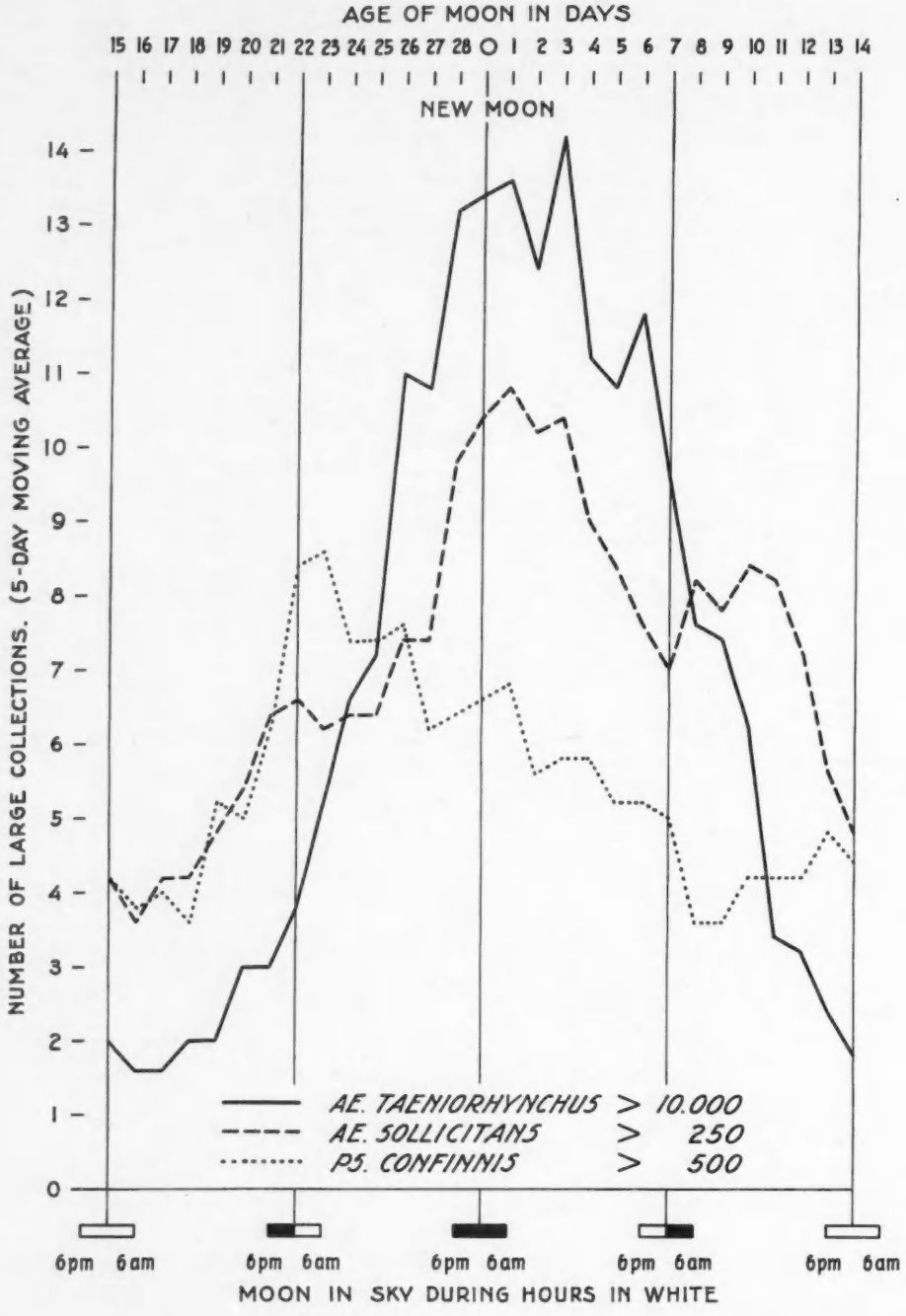
AGE OF MOON IN DAYS
15 16 17 18 19 20 21 22 23 24 25 26 27 28 O 1 2 3 4 5 6 7 8 9 10 11 12 13 14
NEW MOON
NUMBER OF LARGE COLLECTIONS. (5-DAY MOVING AVERAGE)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
AE. TAENIORHYNCHUS > 10.000
AE. SOLLICITANS > 250
PS. CONFINNIS > 500
6pm 6am 6pm 6am 6pm 6am 6pm 6am 6pm 6am
MOON IN SKY DURING HOURS IN WHITE

FIG. 7.—Number of large collections of *Aedes* and *Psorophora* averaged by moon age. Data extracted from a 10-year record of 60 to 110 traps per year operating throughout Florida on a fixed twice-a-week schedule.

come exactly on the new moon whereas troughs appear very consistently within 1 day of full moon. This would be expected if mosquitoes were more active during astronomical twilight (evening or morning) than in the middle of the night, because on full moon night both twilights are brightly illuminated and drastic changes in twilight illumination occur on the first few days before and after full moon, whereas the several nights on either side of new moon show very minute changes in twilight illumination, or at least too little a variation to make new moon night conspicuously unilluminated at either twilight compared to the few days before or after. When the moon segment is large enough to make an appreciable difference in twilight illumination, close to the quarter moon, then collection sizes are affected by night-activity rhythms. This may explain why the curves so often peak near one quarter-moon or both (bimodal curves), and it is reasonable to expect that these idiosyncracies are somehow related to differences between species and sexes (see fig. 3) in twilight activity patterns. In this respect it is recalled that moonlight has been shown to affect the house-haunting habits of female *Anopheles funestus* Giles in West Africa to the extent that the proportion of house entries between sunset and 8 p.m. was six times greater on moonless nights than on nights after full moon (Ribbands 1946). Ribbands also showed that moonrise at any time of the night resulted in a sudden influx of night entries. It has also been shown that *Anopheles gambiae* Giles, *Aedes africanus* (Theobald), and *Chrysops centurionis* Austen (a tabanid fly) initiate their biting activity in the Uganda forests earlier on moonless nights than on moonlit nights, the latter being defined as those nights when the moon's disc was more than 10 percent illuminated and above the horizon during all of the first hours following sunset (Lumsden, 1952). Such facts, in conjunction with the realization that at least ovipositing mosquitoes can distinguish between light intensities as low as one-quarter that of starlight (Thompson 1940), are adequate evidence that the attractant power of a light trap is superimposed on natural illumination patterns the most minute details of which are recognizable to the insects.

SUMMARY

Long series of New Jersey light-trap operations in Florida are analysed for lunar cycle periodicities. Higher collections at new than at full moon are demonstrated for *Anopheles*, *Culex*, *Mansonia*, *Uranotaenia*, *Deinocerites*, *Aedes*, and *Psorophora* mosquitoes. The ratio of collection size between peak near new moon and trough near full moon varies among species and observational periods from 2:1 to 14:1, averaging 6:1. In *Aedes taeniorhynchus* and *Deinocerites cancer* a pronounced lunar periodicity occurred in light-trap collections while nonattractant air-sampling devices showed no such periodicity. This lack of evidence for a moon-phase effect directly on flight activity, the limited range of the new/full moon ratio among mosquito species, and the similar ratios obtained for as disparate insects as mosquitoes and noctuid moths, strongly supports the contention that lunar periodicity in light-trap captures of any night-flying insect is not the result of increased flight activity at new moon as such but rather the result of a purely physical cycle in the attractant efficiency of the light trap superimposed on night-activity patterns governed by minute changes in natural, moon-determined night illumination.

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INFLUENCE OF HEIGHT AND STAGE OF DEVELOPMENT OF DENT CORN ON OVIPOSITION BY EUROPEAN CORN BORER MOTHS

RAY T. EVERLY[1]

ABSTRACT

Studies conducted at Lafayette, Indiana, indicated that the relationships between these factors and the number of eggs laid are curvilinear and best expressed by a second-degree parabola where $Y_c = A + BX + CX^2$. In the effect of stage of development the coefficients of the X and X^2 terms were negative and positive, respectively, whereas in the effect of height the sign of the X^2 term was negative. On early-planted corn 15 percent of the eggs deposited by second-generation moths were laid on the ears. In all, about three times as many eggs were deposited on late-planted corn, but only 1 percent of these were laid on the ears and the number laid on the leaves increased correspondingly. A theoretical curve of oviposition based on the data from these studies showed that for 10 days before and after midsilking height at midoviposition and stage of development (as measured by the date of midsilking) both are effective and are highly correlated with each other.

The major factors that affect the attractiveness of corn to the European corn borer (*Pyrausta nubilalis* (Hbn.)) are its inherent characteristics and its height and stage of development during the period of oviposition. Environmental conditions such as soil fertility and tilth, rainfall, and temperatures influence the amount of oviposition principally through their effect on height and stage of development. When oviposition occurs early in the development of the corn plants, height is the most important. When it occurs later, approaching the period of tassel appearance, stage of development becomes a greater influence. However, height may be also of importance during late-summer oviposition for corn that has been planted very late. It should be recognized that these two factors represent conditions within the plants that affect their attractiveness to the moths, and are not in themselves the reasons why some corn is heavily infested and other corn is relatively free of corn borers.

This variation in the attractiveness of corn at different stages of development was recognized by the earliest investigators. Krasslistchik (1916), a Russian entomologist, recommended that an early American variety, Longfellow Flint, be sown as a trap crop. Ficht (1931) reported the effects of height on oviposition and recommended adjusting the planting date as a means of corn borer control. Olfactometer tests by Marston and Dibble (1930) indicated that corn borer moths were more strongly attracted to corn 24 to 36 inches tall than to corn 2 to 8 inches tall. Patch (1942) showed that the effect of height differences on oviposition increased as the plants became taller and differences in height became greater. Present-day recommendations of time of planting as a means of corn borer control are based upon the recognition of the effect of height and stage of development on oviposition as well as survival of the larvae.

Investigations on the influence of height of corn and stage of development, on oviposition by corn borer moths were conducted at Lafayette, Indiana in 1944, 1945 and 1946.

MATERIALS AND METHODS

In 1944 two inbred lines were used, but in 1945 and 1946 two single-cross hybrids were substituted because of their greater vigor and attractiveness to corn borer moths. In 1944 corn was planted on April 21, May 3, 10, and 16; in 1945 on April 20, May 5, 19, 29, and June 2; and in 1946 on April 19, 30, May 9, 16, and 23. In 1945 a fifth planting was added for the study of second-generation oviposition, and in 1946 to give a wider range of plant heights for first-generation studies.

Plots consisted of three single-plant hills. To avoid competitive effects of adjacent plantings, a single corn row was left unplanted around each plot.

Egg counts were made at 3-day intervals throughout the oviposition period. Height measurements of the corn plants were taken, to the extended tip of the longest leaf, as nearly as possible at the middle of the oviposition period, since Meyers et al. (1937) found that height of corn at this time gave the highest correlation with the number of eggs laid.

The mean silk date was obtained by observing daily and tagging each plant with the date the first silk appeared.

To facilitate germination and obtain a wider and more nearly uniform spread of plant heights, the early plantings were covered at the time of planting with commercially prepared domes of semi-opaque, specially treated paper. These domes acted as miniature greenhouses and protected the young plants from adverse growing

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Table 1.—Average numbers of eggs laid by European corn borer moths and midoviposition heights of corn plants in relation to dates of planting. Lafayette, Indiana.

Planting	1944		1945		1946	
	Eggs per plant	Average height	Eggs per plant	Average height	Eggs per plant	Average height
	Number	Inches	Number	Inches	Number	Inches
First.....	29.8	29.0	39.8	21.9	144.3	37.7
Second.....	22.8	27.2	32.2	20.4	77.8	32.0
Third.....	10.8	23.4	18.8	16.2	56.0	28.6
Fourth.....	1.9	17.6	0.9	9.8	45.6	28.0
Fifth.....	No	planting	Plants	had not emerged	14.2	20.9

Planting dates were as follows: 1944—April 21, May 3, 10 and 16.
1945—April 20, May 5, 19, 29 and June 20.
1946—April 19, 30, May 9, 16, and 23.

conditions. Each planting was made as the plants of the preceding one emerged from the soil.

The experimental design in 1944 consisted of two 8 x 8 Latin squares with the four planting dates and two inbred lines completely randomized. In 1945 and 1946 the planting dates and hybrids were arranged in completely randomized blocks and replicated 10 times.

EFFECT OF PLANT HEIGHT ON OVIPOSITION

Table 1, giving the average data for the inbred lines and single-cross hybrids used, shows that the number of eggs laid increased with the height of the corn. The season of 1945 was cold and late and is reflected in the shortness of the corn, whereas the best growing conditions occurred in 1946. When these data were plotted and regression lines fitted (figure 1), it was found that the relationship was curvilinear. A study of the data indicated that the function was of the parabolic type and second-degree parabolas were fitted. It will be noted that the curves are all of the generalized type, where $Y_c = A + BX + CX^2$, with a negative coefficient for X and a positive one for X^2.

Previous investigators have assumed that the relationship between the number of eggs laid and the height of corn plants during the oviposition period is linear. Many of the data presented by them involved a restricted range in plant height, or the curvilinearity of the relationship was obscured by the use of many varieties of different degrees of attractiveness. When varieties representing a narrow range in plant heights are compared, a linear correlation introduces little error in the interpretation of the results.

Since the data obtained at Lafayette indicated a consistent curvilinear relationship, the data presented by earlier investigators were re-examined for similar relationships. Those of Neiswander and Huber (1929) were recalculated, and their results are presented in figures 2 and 3, together with the linear regression lines fitted by them as well as second-degree parabolas. The much closer fit of the data to the second-degree parabola equation than to the linear one is quite evident. Using the standard errors of estimate for the two lines as a measure of the goodness of fit, the curvilinear regression reduces the standard errors of estimate in the 1927 data from 1.373 to 0.224, and in the 1928 data from 1.429 to 0.996.

Data from a date-of-planting experiment conducted by Patch (1929) at Sandusky, Ohio, are presented in figure 4, with the straight-line and curvilinear regressions. Here again, the better fit of the curvilinear regression is quite evident. The standard errors of estimate are reduced from 3.217 to 1.133.

Ficht (1931) presented similar data for experiments conducted at Monroe, Michigan, under single-generation infestation, when the peak of oviposition occurred around July 15 to 20. As shown in figure 5, for 1928 and 1930 the relationship between the variables followed the same general second-degree parabolic curvilinearity as the data previously presented. In 1929 the data from the earliest planting deviated from the expected pattern and, although receiving the greatest number of eggs, this planting was 5 inches shorter during the oviposition period than corn planted 10 days later. Several factors probably influenced the oviposition in this locality in 1929. According to the author, it was due to the "reduced vigor of the early planting resulting from cold wet weather immediately following the seeding." This unfavorable condition undoubtedly slowed the growth of the early-planted corn and the planting 10 days later under more favorable conditions surpassed the early planting in height. Further examination of his data shows that the midsilking dates for the May 10 and 20 plantings were July 20 and 27, respectively. Thus at the peak of oviposition the early planting was approximately 50 percent silked and stage of development probably accounted for the increased

Table 2.—Comparison of correlation coefficients for the midsilking date on height of corn at midoviposition, number of eggs laid on midsilking date, and number of eggs laid on height of corn at midoviposition. Data from Meyer *et al.* (1937).

Variables correlated	Table 3	Table 5	Table 6	Table 10	Table 11
Date silked/height	−0.50**	−0.30	−0.55**	−0.63**	−0.72**
Eggs laid/date silked	−0.43**	−0.18	−0.59**	−0.69**	−0.60**
Eggs laid/height	0.62**	0.45**	0.59**	−0.72**	0.75**

**Significant at odds of 99:1.

oviposition. Today in most areas infested by the corn borer in this hemisphere, multiple generations exist. Consequently the first generation occurs at least a month earlier and the corn development has much less influence than it did when Ficht made his studies. Height of the corn at the time of midoviposition is now the best index of its attractiveness, and the 1929 results of Ficht do not invalidate the relationship of height of corn to the numbers of eggs laid.

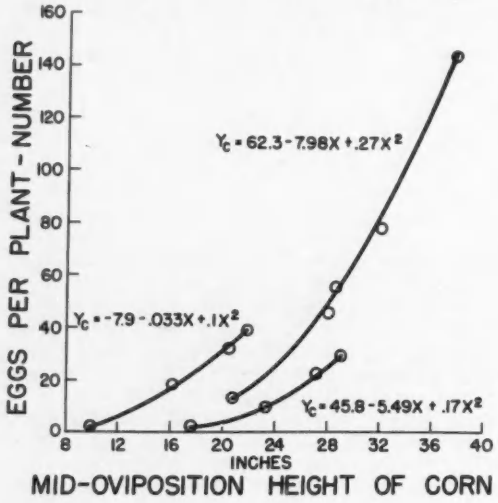

FIG. 1.—European corn borer eggs laid during early summer period of oviposition on corn planted at different times in 1944, 1945, and 1956. Lafayette, Ind.

Not only do the foregoing data support the curvilinearity of the relationship of height and the number of eggs laid, but the equations for the second-degree parabolas that are fitted to these data are similar to those of the date-of-planting studies at Lafayette, having the same signs for the coefficient of X^2 in the equations. However, though the basic relationship is curvilinear, linear regressions give a high degree of correction for data with a relatively narrow range of plant heights. This is particularly true at high levels of oviposition and in those experiments where curvilinearity of the relationship may be obscured by inherent differences in attractiveness of the corn strains. Where practical, evaluation of the relative attractiveness of different kinds of corn should be based upon the deviations of the observed numbers of eggs deposited per plant from the regression curve as established on the basis of planting-date averages.

EFFECT OF STAGE OF DEVELOPMENT ON OVIPOSITION

There are few published data on the effect of plant development on the numbers of eggs laid during late summer. Beard (1943) studied ovi-

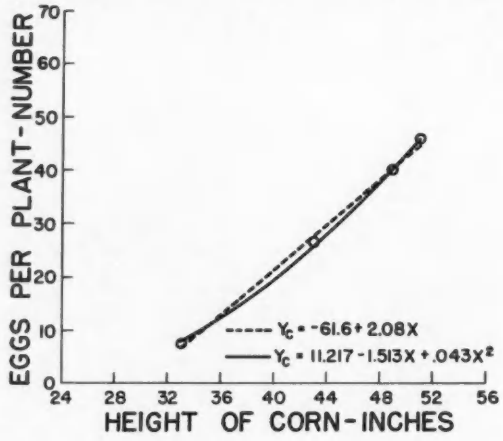

FIG. 2.—European corn borer eggs laid on corn of different heights in 1927. Data from Neiswander and Huber (1929).

position on 14 planting dates with two varieties of sweet corn in relation to definite periods of plant growth which were then in use and which were later published by Batchelder (1949). However, there was no simple way to measure quantitatively this system of identification of stage of development or to relate the different planting to a fixed focal point of reference. Other workers (Luckmann and Decker 1952; Beard and Turner 1942) developed methods of study of stage of corn growth, but related these primarily to larval survival rather than oviposition. The tassel-ratio criterion developed by Luckmann and Decker has the added disadvantage that the plant must be

destroyed to measure its development, thus preventing further studies with individual plants. This also presupposes very uniform study material and practically eliminates double-cross corn in critical studies. Even if used, it would require much larger plots, with additional labor for egg examinations. The date of midsliking is the simplest way to compare widely divergent varieties and planting dates.

Under multiple-generation conditions the possibility of maturity having a modifying effect on

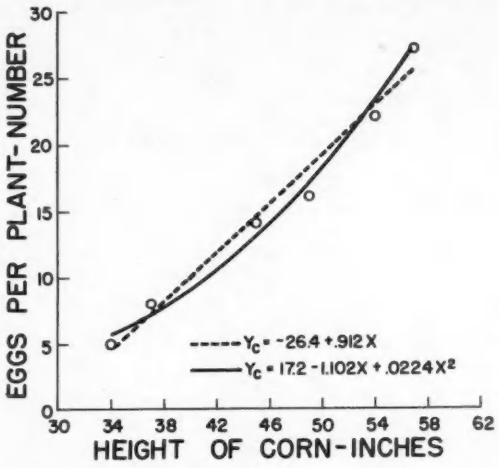

FIG. 3.—European corn borer eggs laid on corn of different heights in 1928. Data from Neiswander and Huber (1929).

oviposition is much less during the early summer, but correspondingly greater during the late summer. The height of corn at midoviposition is usually highly correlated with its maturity index, as shown by Meyers et al. (1937). If oviposition occurs just prior to silking, only a multiple correlation analysis can determine whether height or maturity had the greater influence on the number of eggs laid.

A comparison of the correlation coefficients for corn height at midoviposition, midsilking date, and number of eggs laid from five experiments reported by Meyers and his coworkers is given in table 2. In all their studies where these three coefficients can be compared, the correlation between height and eggs laid is highly significant and equals or exceeds the correlation between midsilking and eggs laid. In the data from their table 5 the correlation coefficient between the date of silking and the number of eggs laid and the date of silking and height are nonsignificant, whereas that between the numbers of eggs laid and the height is highly significant. Without the data on which these correlation coefficients are based, it is impossible to determine, in those cases where both relationships are significant, which of the two correlations is responsible for the variations in the number of eggs laid. However, since their experiments were carried out under single-generation conditions, it is reasonable to assume that under multiple-generation conditions, when egg laying occurs 1 month earlier in the development of the corn plant, stage of development as represented by the midsilking date would have less influence.

Table 3.—Eggs laid during the late summer on corn planted on different dates, with height of corn at midoviposition and mean silk date. Lafayette, Indiana, 1945.

Planting date	Eggs laid per plant	Height at midoviposition (August 16)	Time from July 1 to midsilking
	Number	Inches	Days
April 20	25.1	82.4	29.1
May 5	29.6	82.9	30.8
19	45.0	84.2	34.3
29	61.6	83.7	40.6
June 20	82.0	76.2	51.3

In 1945 at Lafayette the date-of-planting studies were continued through the period of late-summer oviposition. A late planting on June 20 was added to obtain a stage of corn development comparable to that of early May plantings at the time of early-summer egg laying. The data from this experiment are given in table 3. At the time of egg laying the corn planted in April and early May had attained its maximum height and only the ears were growing

Table 4.—Relation of midsilking date to the number of eggs laid on different parts of the corn plants. Lafayette, Indiana, 1945.

Date of midsilking	Leaves		Stems and leaf sheaths	Ears	Total eggs laid per plant
	Upper surface	Both surfaces			
	Percent	Percent	Percent	Percent	Number
July 29	3.19	83.13	1.83	15.04	25.1
31	4.31	86.83	1.88	11.29	29.6
August 3	3.49	85.53	2.59	11.88	45.0
10	5.27	91.40	2.52	6.08	61.6
20	7.73	97.09	1.74	1.17	82.0

and developing. Corn planted in late May and June was still increasing in height and was approaching the period of pollen shedding, with ear shoots present on practically all plants. The similarity of heights in the first four plantings indicates that height differences were not a factor influencing oviposition. However, to eliminate the possibility of some influence due to height, a multiple correlation analysis was made. This analysis indicated that the differences in the number of eggs laid were due almost entirely to the stage of development and that the effect height was negligible.

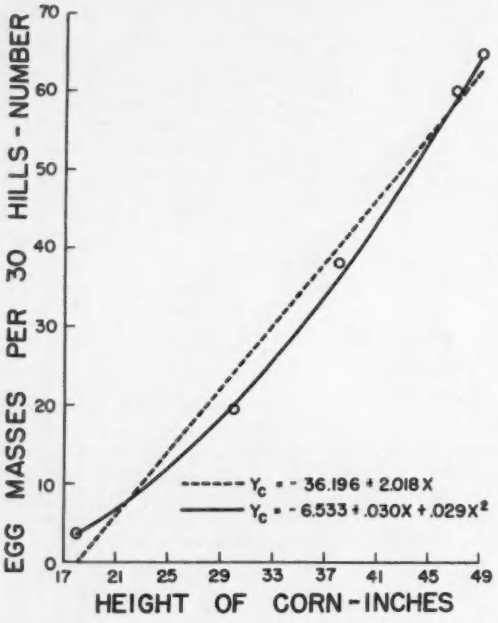

FIG. 4.—The effect of height of corn planted on five dates on the number of eggs laid by European corn borer moths in 1928. Data from Patch (1929).

The data showing this relationship between the numbers of eggs laid and stage of development as measured by the midsilking date are plotted in figure 6. It is evident that this relationship is curvilinear. It is of the second-degree parabolic type, similar to that for numbers of eggs and height, except that the coefficient of X^2 is negative, the reverse of that found for height and eggs.

DISTRIBUTION OF EGGS ON CORN

In this experiment a record was kept of the numbers of eggs laid in each mass and the location of the mass on the plant. Sites recorded were the upper and lower leaf surfaces, stems and sheaths, and ears. In table 4 these data are summarized as percentages of the total number

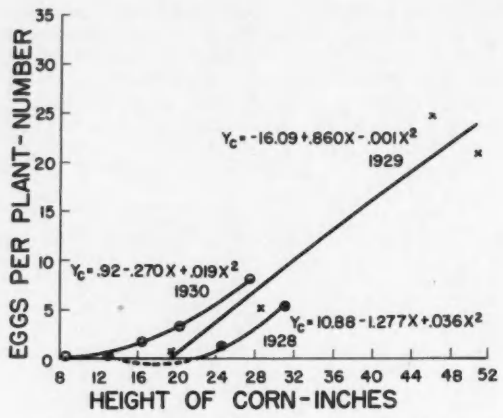

FIG. 5.—Effect of height of corn planted on different dates on oviposition by European corn borer moths in 1928, 1929, and 1930. Data from Ficht (1931).

of eggs laid for each date of midsilking for the different plantings. The shift in egg depositions at the various sites for the different dates is shown in figure 7. These data indicate a marked increase in the proportion laid on the ears as the plant development advances. On corn that silked on July 29, 15 percent of the eggs laid were placed on the ear, compared with 1 percent on corn that silked on August 20. Although approximately three times as many eggs were laid on the plants of the later maturing corn, proportionally 15 times as many were laid on the ears of the earliest maturing corn plants.

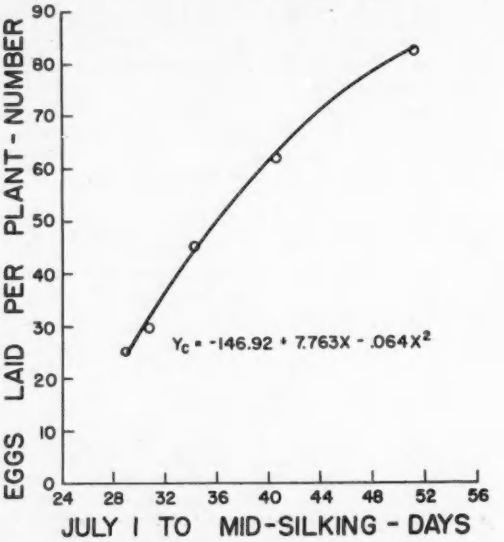

FIG. 6.—Effect of stage of plant development of corn planted on different dates on the numbers of eggs laid by European corn borer moths in 1945. Lafayette, Ind.

According to Meyers (1930), approximately all ears of a variety silk within 4 days of the midsilking date. This would mean that the ear shoots were present on nearly all the plants in the latest planting and that silks had begun to appear by August 16 with all ears showing silks by August 24. As shown in table 5, second-generation egg laying began on August 6. On August 16, 7.4 percent of the total eggs had been laid. During the 8-day period when silks were appearing on this late planting, 48 percent of the eggs were laid. After silking was complete 45 percent were laid. It appears then, that the lack of ears in the late plantings was not a factor in the proportion of eggs laid on the ears of the different plantings.

Table 5.—Accumulated numbers and percent of total eggs laid on dates of examination of corn plants during late-summer oviposition period. Lafayette, Indiana, 1945.

Date	Accumulated total eggs	Portion of total eggs laid
	Number	Percent
August 6	231	0.8
11	634	3.0
16	2124	7.4
20	12079	42.0
23	15956	55.5
27	20566	71.5
30	25210	87.7
September 3	27417	95.3
7	28759	100.0

Analyses were made of the correlations of the percentages of eggs laid on the different sites and the midsilking dates of the different plantings. The constants for these analyses are given in table 6. It will be noted that only the percent of eggs laid on the stems and sheaths was not significantly correlated with the midsilking date. Also, the regression coefficients for the percent of eggs laid on the ears and those laid on the leaves were almost identical in magnitide but different in signs, indicating that the decrease in the percent laid on the ears was equal and corresponded to the increase in the percent laid on the leaves.

The eggs laid on the stems and leaf sheaths showed no trend of increasing or decreasing toward early or late planted corn. The percent laid on the upper surface of the leaves was fairly constant for the first three plantings, but showed a significant increase on the two later plantings (table 4).

This tendency to oviposit in greater numbers on the ears of early planted corn may account for the high ear infestation and droppage before harvest in some years, as the percentage of eggs laid on the ears may be greater in seasons when late-planted corn is not abundant. In addition, the availability of the silk and kernels as favored feeding sites may result in higher survival of the larvae hatching from these eggs, thus causing

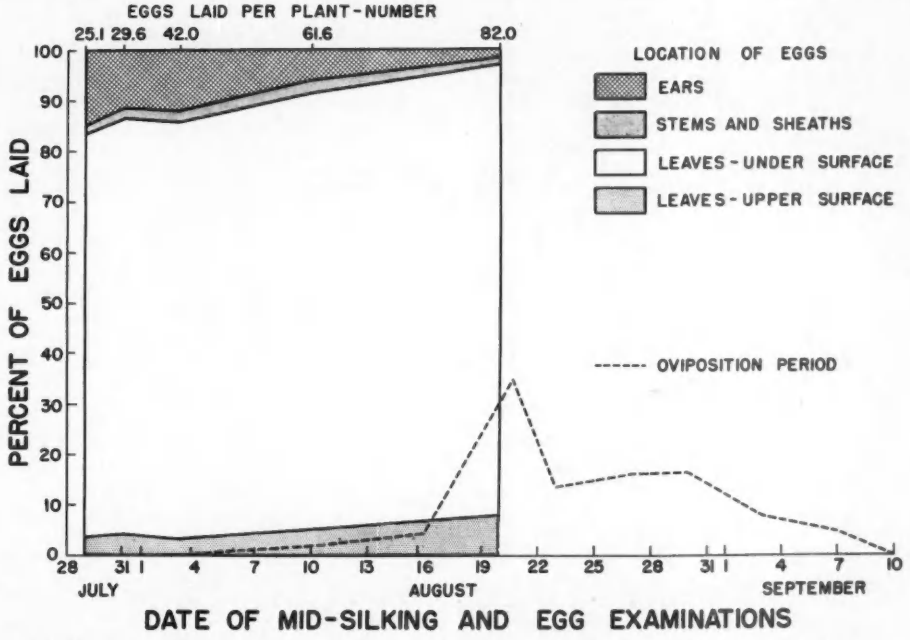

FIG. 7.—Percent of eggs laid by second-generation European corn borers on different parts of corn plants in relation to time of mid-silking and oviposition. Lafayette, Ind. 1945.

further yield reduction through direct damage to the ear and the production of chaffy ears as well as greater ear droppage from borer feeding in the shanks.

These studies indicate that two principal factors operate to modify the numbers of eggs laid on corn plants by corn borer moths. Height is the primary factor during the early-summer oviposition, but stage of development as measured by the midsilking date is chiefly responsible during the late-summer egg-laying period. During the period of plant development just prior to tassel appearance and immediately following pollen shedding both factors may be operating, and only multiple-correlation analysis can determine which is chiefly responsible. During this time height at midoviposition and midsilking date are often highly correlated.

Table 6.—Correlation and regression constants for mean date of silking and the percent of eggs laid, for various parts of corn plants. Lafayette, Indiana, 1945.

Location of eggs	Y-intercept (A)	Regression coefficient (b)	Correlation coefficient (r)	r^2
Upper leaf surfaces	−2.40	0.193**	0.954**	0.91
Both leaf surfaces	66.63	0.596**	0.972**	0.94
Stem and leaf sheath	5.16	−0.087	0.015	0
Ears.....	31.09	−0.591**	0.974**	0.95

**Significant at odds of 99:1.

Neiswander and Huber (1929), in discussing silking (stage of development) and oviposition by corn borer moths, found a correlation of −0.91 between these two variables, which they state was "significant for odds of 615:1." They continue, "—this high correlation might lead to the conclusion that date of silking as such, greatly influenced the moths and consequently the numbers of eggs deposited. However, in this instance, silking includes more than stage of plant development as such. Where six varieties are made the equivalent of one variety on successive dates of planting, a high correlation between silking and eggs can be expected, for the correlation between silking and height is high."

Where multiple generations of corn borers exist there is a shift from the influence of height on oviposition during the early development of the corn to that of stage of development as measured by the midsilking date in the post-pollination period. Thus, if we had corn in all stages of development present in the field during oviposition, we would expect the most eggs to be deposited on that corn at or just prior to pollen shedding and decreasing numbers on the plantings that had been made earlier and later. Data obtained by Beard (1943), showed that when all stages of plant development are present, the greatest number of eggs are laid during the S-1 period when pollen shedding begins, and less eggs are laid as maturity is approached and as the stage of development becomes earlier, with practically none on the seedling and pre-whorl stages. A theoretical egg deposition curve is shown in figure 8. The portion of the curves lying between the point where stage-of-development influence begins and height influence ends would receive the heaviest oviposition. Beyond these two points the number of eggs laid would gradually decrease until no eggs would be found on corn too small to be attractive or on corn that was unattractive because of its advanced maturity as indicated by dry stalks and leaves.

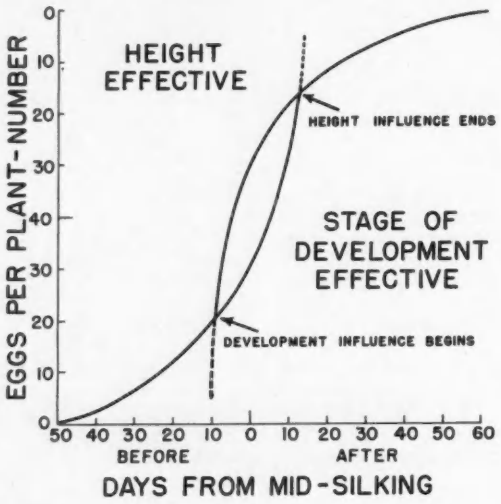

FIG. 8.—Combined influence of height and maturity on the numbers of eggs laid by corn borer moths when the peak of egg deposition occurs at different times during plant development.

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ANTENNAL HYGRORECEPTORS OF THE MILKWEED BUG, ONCOPELTUS FASCIATUS (DALLAS) (HEMIPTERA, LYGAEIDAE)[1]

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ABSTRACT

Various portions of the antennae, mouth parts, and legs were painted with shellac to inactivate possible hygroreceptive areas thereon, and the times required by the insects to locate water following these various treatments were recorded. Through a process of elimination the distal part of the fourth antennal segment was found chiefly responsible for hygroreception. Supporting evidence for this was obtained through use of an olfactometer. Sections through the antennae showed considerably more nervous tissue in the fourth segment than in the others.

In recent years increased attention has been paid to the relation between insects and their physical environment. However, aside from the researches of a few investigators on a small number of forms, we have little detailed knowledge of hygroreception in insects. Little uniformity exists in the type of receptor employed for water detection in various species of insects. A type of end organ acting in a hygroreceptive capacity in one species may not occur on another species or act in the same capacity thereon (Slifer 1954). From this it would appear that before any generalizations can be made, the location and structure of hygroreceptors must be determined for a great many species. The purpose of this study, therefore, was to determine the site and structure of the hygroreceptive organs on the common milkweed bug, *Oncopeltus fasciatus* (Dallas), and to observe the behavior of the insect when various portions of the antennae, mouth parts and tarsi and/or their combinations were inactivated.

The volume of literature relating specifically to hygroreception in arthropods is not large. However, some interesting papers have appeared during the last 15 years. A survey of the literature reveals that the location and type of various hygroreceptive organs is not specific but in fact quite varied.

Gunn (1937) working with the wood louse, *Porcellio scaber* Lat., de ected hygroreceptive organs in the thoracic region but did not identify them as to a specific type. Lees (1948), working with *Ixodes ricinus* L., presented evidence which indicated that trichoid sensillae distributed in the anterior pit of Haller's organ were hygroreceptive in nature. Bursell and Ewer (1950) discovered hygroreceptive areas both on the general body surface and on the antennae of the onychophoran, *Peripataopsis moselyi* (Wood-Mason).

Pielou (1940) identified the hygroreceptors of the adult mealworm, *Tenebrio molitor* L., as being pit-peg organs on antennal segments 1–10, and peg organs on segments 6–11. In the louse, *Pediculus humanus corporis* DeGeer, the hygroreceptors are small cones bearing four minute hairs (tuft organs) and are located on the fourth and fifth antennal segments (Wigglesworth 1941). In the wireworms of the genus *Agriotes* Esch., the presence of the antennae plus the maxillary and labial palpi were found to be necessary for a normal humidity response (Lees 1943). Lees pointed out that he could not associate the response with any specific sensillae. The hygroreceptors of the spider beetle, *Ptinus tectus* Boie, have been localized on the antennae but have not been identified (Bentley 1944). Begg and Hogben (1946) suggested that surface cones on the antennae of *Drosophila melanogaster* Meigen functioned as hygroreceptors although similar functioning organs may be present on other parts of the body. Roth and Willis (1951a) observed two types of thin-walled sense organs, basiconic and trichoid sensillae, on the antennae of six species of beetles belonging to the genus *Tribolium*. Roth and Willis (1952), working with *Blattella germanica* (L.) and *Aedes aegypti* (L.), observed

[1]Published with the approval of the Director as Paper No. 838, Journal Series, Nebraska Agricultural Experiment Station. Accepted for publication July 11, 1958.

that the antennae in both species were hygroreceptively active. Such activity could be correlated with the antennal distribution of thin-walled sensilla (trichoid and/or basiconic).

Unsuccessful attempts to identify the sites of hygroreceptive activity have been made by Thomson (1938) on the mosquito, *Culex fatigans* Wiedemann, and by Gunn and Cosway (1938) on the cockroach, *Blatta orientalis* L.; the latter workers suggested that hygroreceptors may be located on the antennae of the roach.

EXPERIMENTAL

The common milkweed bug was employed as the test insect in the following experimental work. The insects were reared in essentially the same manner as that described by Andre (1934). For the purposes of these experiments the rearing containers were examined daily to remove the eggs which are conveniently laid on top of the cheesecloth container cover and to remove the newly moulted adults. The young adults were placed in holding jars containing food and water for a period of 5 days prior to testing. This technique assured a uniform adult age for test purposes.

In locating the hygroreceptor sites the entire antennae, or portions of the antennae, were painted with shellac, thus rendering them nonfunctional to the insect as hygroreceptive organs. For the purposes of this study the antennal segments were numbered from one through four; segment number 1 is the proximal segment, the distal segment is number 4. In addition to the antennal painting, various combinations of the mouth parts and tarsi in conjunction with the antennae were covered with shellac. The shellac had previously been colored with eosin dye, making the treated areas readily discernible under the microscope. Other covering substances, such as a collodion and acetone mixture, were tried without success. The painting of the various appendages was accomplished while the insects were under carbon dioxide anesthesia. Some individuals, upon recovering from the anesthesia, were able to rid themselves of the shellac coat by secreting copious quantities of salivary fluid or by a continuous process of pressing and rubbing the appendage in question against the floor or wall of the petri dish in which they were contained. Such insects were consequently withdrawn from the experiment.

After the insects were treated as above to inactivate the desired portion of the body, they were placed in petri dishes and deprived of food and water for 3 days. For every treated or shellacked insect an untreated or control insect was used, the latter held in a separate petri dish. Upon termination of the starvation period, a piece of dental wick 1.2 cm. in length was saturated with water and placed on end in the center of the petri dish. The total elapsed time was recorded from the moment the dental wick was placed in the petri dish until the onset of drinking. The upper time limit for locating the water-soaked wick was arbitrarily set at 180 minutes. Insects whose mouth parts were painted with shellac and could not ingest water were timed to the point of finding the water-saturated wick whereas insects painted in areas other than the mouth parts were timed to the point of actual water ingestion.

The results of 15 individual experiments involving 60 insects each (30 test insects and 30 control insects) and designed to locate the hygroreceptive areas by the previously described method are shown in figure 1. For any given area treatment two sets of 30 insects each were treated on different days, thus giving a total of 60 insects per treatment.

Figure 1 indicates that insects having the fourth antennal segment covered with shellac required a much longer period of time to find the water-soaked dental wick than the untreated controls. Further examination points out that when the distal one-half of the fourth antennal segment was painted the insects required an average of 132 minutes to find the wick. This time interval is comparable to that required for those insects whose entire antennal segments were painted. These data strongly suggest that the chief hygroreceptive area is located on the distal one-half of the fourth antennal segment.

Shellacking the mouth parts and tarsi appeared to have no significant effect except to hinder water ingestion. This would appear to indicate that hygroreceptive organs are not located on the mouth parts or tarsi.

Olfactometer Experiments.—Substantiating evidence as to the location of the hygroreceptors in

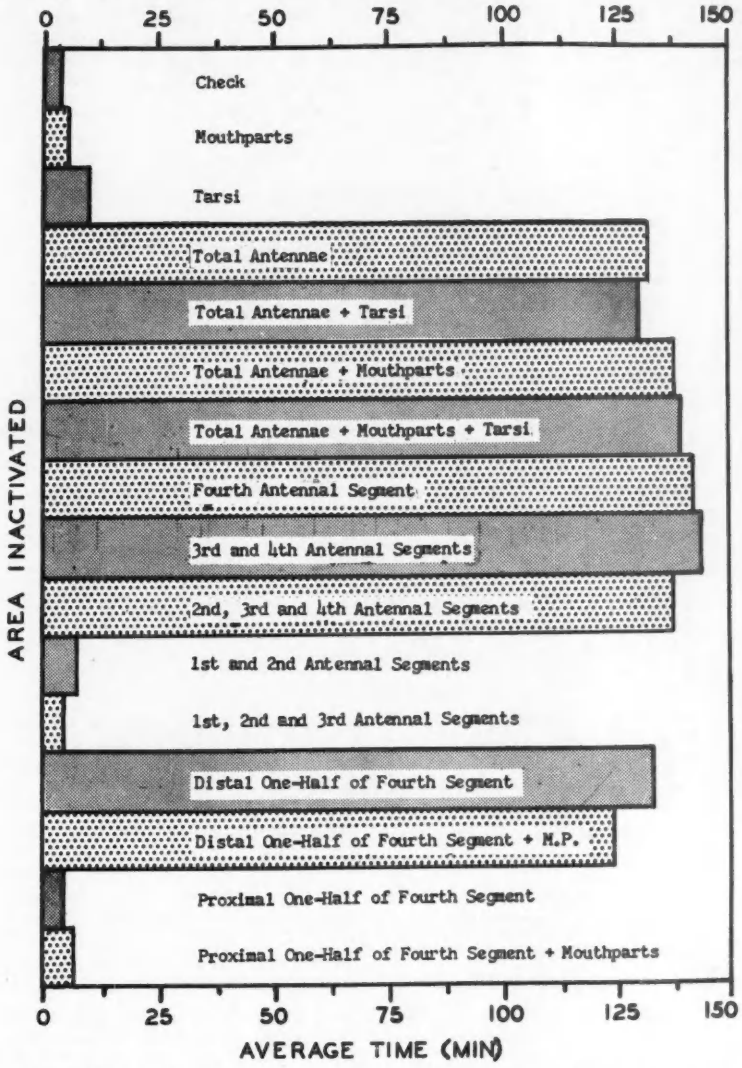
Table 1.—Choice and average time (min.) spent in indicated areas of the olfactometer for *Oncopeltus fasciatus* (Dallas) having the distal antennal segments covered with shellac as compared with control insects.

No. insects tested	Percent of insects choosing			Average time remaining in		
	Dry	Moist	No choice	Entrance	Moist area	Dry area
Treated—40	57.5	30.0	12.5	11.4	7.0	11.7
Untreated—40 (control)	2.5	91.5	6.0	6.3	18.6	5.1

the milkweed bug was obtained through the use of an olfactometer. The olfactometer used in these experiments was essentially the same as the ones used by Barrows (1907), Frings (1941), and Hafez (1950) in determining the sites of olfactory end-organs on various insects.

The only functional modification of the olfactometer used in this work consisted of drawing rather than blowing the air through the apparatus. A diagrammatic sketch of the olfactometer is presented in figure 2. The olfactometer was constructed of cellulose nitrate sheeting making it possible to constantly observe the test insects. Dried air was obtained by filtering air over anhydrous calcium chloride and the moist air resulted from drawing air through an ordinary distilling tube jacket filled with water. Moist and dry air were then mixed in the entrance area of the olfactometer.

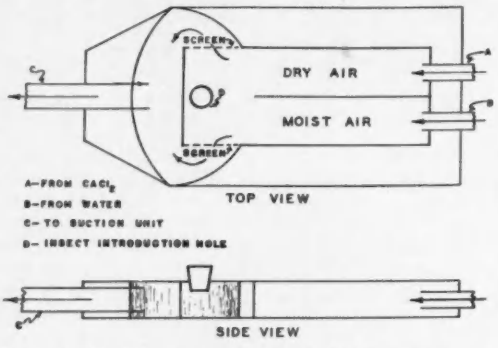
To test the hygroreceptive response in the olfactometer the following procedure was carried out. Treated insects were prepared by covering segments three and four with shellac as before. A control insect was tested for each treated insect.



TEXT FIG. 1.—Average length of time required by starved, adult *Oncopeltus fasciatus* (Dallas) to ingest or detect water following shellac treatment of the indicated area.

In all, a total of 80 insects was tested; 40 were treated and 40 were controls. Following a 3-day period of water privation, the insects were placed individually into the entrance area of the olfactometer and were allowed a maximum of 30 minutes to choose between the moist or dry air. The data in table 1 summarize the results of these tests.

The data set forth in table 1 reveal an area of humidity discrimination located on the two distal antennal segments. The results obtained from the olfactometer tests provide verifying evidence that the hygroreceptive areas are located on the distal antennal segments.



TEXT FIG. 2.—Diagrammatic sketch of the olfactometer.

MORPHOLOGICAL-HISTOLOGICAL STUDIES

The third approach to the general problem was undertaken to explore the possibility of disclosing any correlation between the apparent hygroreceptive activity of the fourth antennal segment and its morphological or histological form. To obtain material for use in studying the external morphology, antennae from newly moulted and adult insects were heated in 20 percent KOH for 20 minutes and then cleared in beechwood creosote. The entire antennae were then mounted in "Euparal." Histological sections of the various segments were made by fixing them in either Bouin's or Zenker's solution (Guyer 1953). The segments were then embedded in a rubber-paraffin mixture (mp. 54°–56° C.) and sectioned at various thicknesses from 5 to 15 microns. The sections were stained with Delafield's haemotoxylin and eosin, or Mallary's Triple Connective Stain. The staining schedules used were modified slightly from those used by Kennedy (1932). The cross- and longitudinal sections of the antennae were studied at 430x and 950x magnifications.

External Morphology.—Microscopic examination of the four antennal segments revealed apparent differences in the dimensions and structure of their cuticular structures. The second, third and fourth segments were covered with setae having thick walls which remained dense after clearing. The setae on the fourth segment by comparison had much thinner walls which appeared opaque following clearing. A measureable difference in the length and width of the setae on the various segments was also observed. The setae on the fourth segment averaged 0.0571 mm. in length and 0.0038 mm. in width whereas the setae on the other three segments averaged 0.0830 mm. long and 0.0059 mm. in width. It appeared that the smaller, thin-walled and more delicate, setae found on the fourth antennal segment could function more effectively as hygroreceptors than those setae on the remaining three segments.

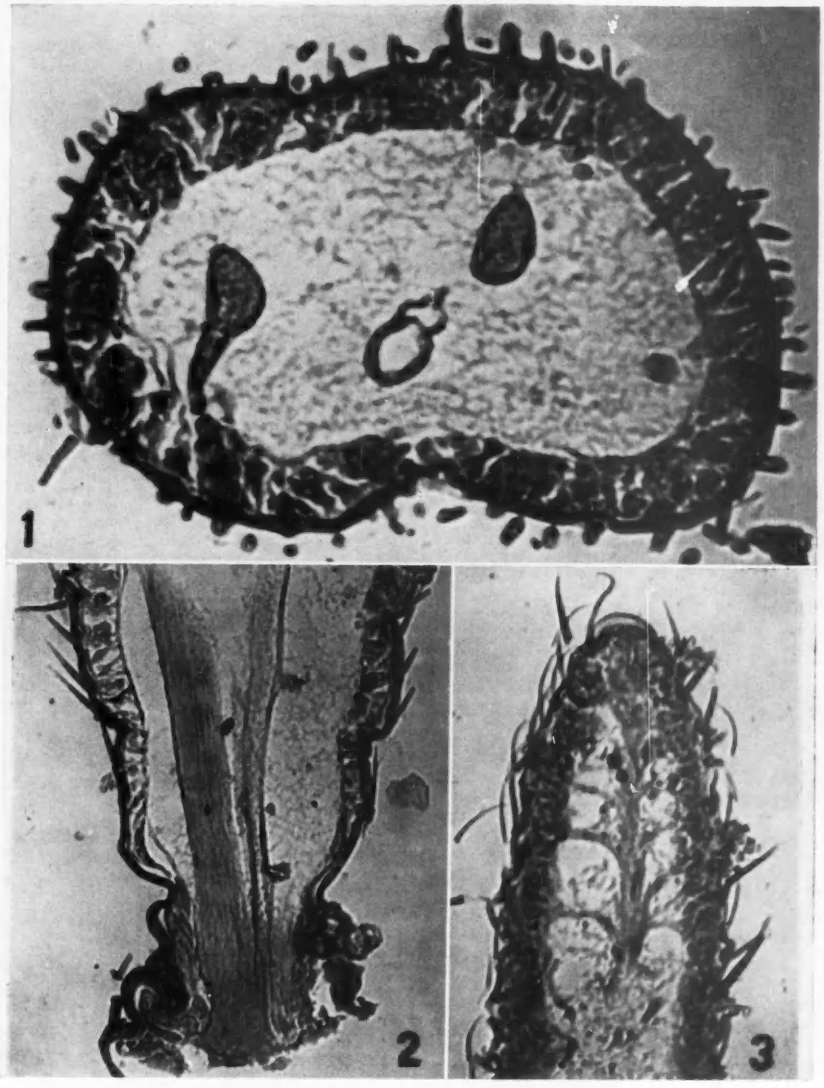
Internal Morphology.—Serial cross- and longitudinal sections of the four antennal segments revealed that the antennal nerve remains as a single trunk until it reaches the basal part of the distal segment. Here it bifurcates and gives rise to two antennal nerves. (Plate 1, figures 1 and 2). The two antennal nerves in turn give rise to many nurons which terminate in sense cells within the cuticle. This treelike branching of the antennal nerves in the distal part of the fourth antennal segment is depicted in Plate 1, figure 3. The proximal part of the fourth segment contains only two antennal nerves and is lacking many of the collateral nerves found in the distal part of the fourth segment. This morphological arrangement of nerve tissue offers further supporting evidence that the distal part of the fourth antennal segment is hygroreceptively more active than any other antennal area.

DISCUSSION

The preceding experimental evidence indicates that the principal hygroreceptors of the milkweed bug, *Oncopeltus fasciatus* (Dallas), are located on the antennae and especially on the distal part of the fourth antennal segment.

The identity of particular hygroreceptors have been established in relatively few insects. In the mealworm, *Tenebrio* (Pielou 1940), the pit-peg organs on the antennae were demonstrated to be hygroreceptive in nature, and in *Pediculus* (Wigglesworth 1941) the "tuft organs" on the antennae were shown to be sensitive to humidity. Roth and Willis (1951a, 1951b) identified certain sensillae on the antennal segments of adult *Tribolium castaneum* (Herbst.) which functioned as hygroreceptors. It would appear from the above findings that end organs possessing various morphological forms may operate as hygroreceptors. The work reported here indicates that setiform organs may also act as hygroreceptors.

Starved, nontreated milkweed bugs were not affected in their ability to locate water. The average time required for starved insects whose mouth parts and tarsi were covered with shellac to find water was not significantly different from that of the untreated insects. In comparison



EXPLANATION OF PLATE I

FIG. 1.—Cross section through the midpoint of the distal antennal segment of *Oncopeltus fasciatus* (Dallas). The two distinct antennal nerves are located in the center and appear to have the same texture as the sensory cells surrounding the periphery. FIG. 2.—Longitudinal section through the distal antennal segment of *Oncopeltus fasciatus* (Dallas). Portions of the two antennal nerves are distinct. FIG. 3.—Parsagittal section through the distal antennal segment of *Oncopeltus fasciatus* (Dallas). The treelike branching of one of the antennal nerves is conspicuous.

there was a highly significant difference between the reaction times of those insects whose entire antennae were painted with shellac and untreated or control insects. From these experiments and others previously reported, it was concluded that the site of hygroreceptive activity in the milkweed bug was located on the antennae. Further experimental results indicated that the distal antennal segment was the primary region of activity.

The results obtained in the olfactometer experiments provide supporting evidence that the distal antennal segment is the principal hygroreceptive site.

The data secured in the histological and morphological studies provide visible and specific evidence that hygroreceptors are situated on the distal antennal segment. The type of cuticular appendage and the quantity of nerve tissue present clearly point out a functional activity which is different from that of the other antennal segments.

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THE LIFE CYCLE OF THE MELON APHID, APHIS GOSSYPII GLOVER, AN EXAMPLE OF FACULTATIVE MIGRATION[1]

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ABSTRACT

This aphid was observed in Connecticut to complete its annual egg-to-egg cycle on *Hibiscus syriacus* L. and *Catalpa bignonioides* Walt. At this latitude secondary hosts are populated by migrants, either from primary host plants or from secondary hosts growing in warmer environments. Both males and females can be produced on the primary host plants. True migrant aphids related to this species produce males only on secondary hosts. Unfavorable environmental periods in the summer are passed as a distinct form. During such periods only small, yellow aphids are observed, and these do not grow or reproduce until favorable conditions are restored. Problems in the designation of type of life cycle and the evolutionary significance of the life cycle of this species are discussed.

The life cycle of the melon aphid has long been in doubt. Recently Kring (1955) demonstrated that the primary host of this aphid was *Catalpa bignonioides* Walt. (Bignoniaceae) and not *Sedum* as indicated by Patch (1925). This conformed to the currently accepted migration pattern of a migratory aphid (Hille Ris Lambers 1950).

True migratory aphids have three traits in common. First, eggs are produced only on a few plant species (the primary hosts), and only viviparous females occur on other host plants (the secondary hosts). Second, primary host plants

[1]Accepted for publication September 22, 1958.

usually are members of older plant families than the secondary hosts. And third, male aphids are produced only on secondary hosts, while the oviparous female aphids are produced only on primary hosts.

The discovery of the melon aphid on Rose of Sharon, *Hibiscus syriacus* L. (Malvaceae), in late April and early May indicated that this plant might be serving as a primary host for this aphid. Rose of Sharon and cotton, *Gossypium herbaceum* (one of the major secondary hosts of this aphid), are both classified in the same family of plants, the Malvaceae. This indicated that the life cycle of *A. gossypii* was more complicated than originally supposed.

Several species of *Hibiscus*, including *H. syriacus*, have already been reported (Olsen 1921) as hosts of the melon aphid. None of these reports mentioned the sexual forms or the eggs of this species. Sanborn (1912) observed that the melon aphid overwintered on *Hibiscus* sp. in greenhouses in Oklahoma without producing sexual forms or eggs. Takahashi (1923) found that this species remained on *H. syriacus* and other species throughout the year on Formosa. Börner (1952) stated that during the winter in central Europe, this species remained in a depressed condition almost unnoticed on weeds and woody plants (viz. *Vitis*).

PROCEDURE AND RESULTS

Examination of Rose of Sharon in the fall of 1954, 1955 and 1956 showed the presence of both female and male aphids that could not be distinguished from the sexuales of the melon aphid collected from *Catalpa*. The males on both hosts were winged. Morphological examination also indicated that the other aphid forms from the two primary hosts were very similar and that the ratio of the measurements of the base to the unguis or tip of the sixth antennal segment conform to those given for the melon aphid by Kring (1955). Eggs laid on Rose of Sharon in October and November hatched in late April and early May. The aphids that emerged from these eggs produced colonies. Replicated, comparative transfer studies were made with aphids from *Hibiscus syriacus* L. and from *Catalpa bignonioides* Walt., using forms that would normally migrate to secondary hosts. Aphids from both host species readily colonized cotton, *Gossypium herbaceum* (Malvaceae), and produced the diminutive, yellow forms described by Wall (1933) on dock, *Rumex crispus* (Polygonaceae). It was difficult to establish the aphid on cucumber, *Cucumis sativus* (Cucubitaceae). Transfers were made readily in both directions between *Catalpa* and Rose of Sharon.

A. gossypii was observed throughout the growing season on both *Catalpa* and Rose of Sharon. *Catalpa* was heavily infested in August 1955. Sexuales were produced both by migrants and by individuals which had remained on the host throughout the growing season.

The aphids oversummering on *Catalpa* in July and August 1957 were all diminutive, yellow aphids. This was an extremely hot, dry period in which the leaves of large *Catalpa* trees wilted during the heat of the day. During this period there was no evidence of growth of these aphids.

To determine if these were aestivating forms of *A. gossypii*, the following test was conducted in the laboratory. Aphids were transferred from *Catalpa* to Rose of Sharon cuttings. These

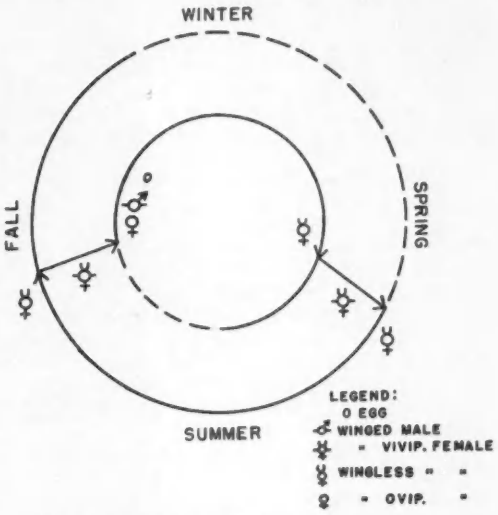

FIG. 1.—Annual life cycle of *Aphis gossypii* Glover in North Temperate Zone. Inner circle indicates primary host plants, outer circle secondary host plants. Broken lines show survival under favorable environmental conditions.

cuttings were growing in either nutrient solution or distilled water. The laboratory conditions were 70° ± 2° F., 30–45 percent relative humidity (not controlled) and 24-hour light. When these diminutive, yellow aphids were transferred to Rose of Sharon cuttings growing in nutrient solution, growth and reproduction resumed. The new generation was composed of the multicolored forms characteristic of this species on *Catalpa*, cotton, melon, and Rose of Sharon. By contrast, transfer of aphids from *Catalpa* to Rose of Sharon cuttings in distilled water resulted in limited growth and reproduction of the aphids. In all but one instance these forms remained yellow in color and diminutive in form. Each transfer was replicated 10 times. During these tests the aphids remaining on the original plant in the natural environment did not change in shape or appearance.

DISCUSSION

The small, yellow aphids observed on *Catalpa*

appear to be the aestivating form of this species. This is also the form that the aphid takes under other unfavorable conditions. Paddock (1919) recognized that this form had a place in the seasonal history but did not describe it. Wall (1933) observed that light forms were characteristic both of dense populations and unfavorable hosts. He also showed that light forms exhibited reduction in size and in segmentation of the antennae.

Aestivation in a more specialized form occurs among species of the aphid genus *Periphyllus* (Essig and Abernathy 1952).

The occurrence of a primary host, Rose of Sharon, in the family of one of the major secondary hosts, cotton, complicates the consideration of the life cycle of this species. It appears that this life cycle may be a combination of the possibilities outlined by Hille Ris Lambers (1950) for polyphagous species. In a sense, this species qualifies as a migrating species (figure 1), in that migration occurs (Kring 1955) from a primary host in the Bignoniaceae to secondary hosts in the Malvaceae, Polygonaceae and Cucurbitaceae. It is now shown that the aphid can also be transferred from a primary host in the Malvaceae to secondary hosts in the Polygonaceae and Cucurbitaceae. However, the aphid can and does remain on both primary hosts throughout the year. It also readily utilizes perennial and annual plants in the Malvaceae as primary and as secondary hosts (*Hibiscus* to *Gossypium*).

Since both sexuales of the melon aphid can be produced on the primary host, and since in the related aphids in this group the designation "true migration" (Hille Ris Lambers 1950) is restricted to species in which males are born on the secondary host prior to migration to the primary host, this species would be designated as a nonmigrating polyphagous aphid. Evans and Gyrisco (1956) demonstrated that barriers can exist within a family and that the pea aphid should be considered a migrating aphid. For the melon aphid such a barrier may exist between secondary hosts in the Cucurbitaceae and the primary hosts. The difficulty in transfer of this aphid from any host, except another Cucurbitaceae, to cucumber was also shown by Paddock (1919) and Isely (1946).

The term migration as used here and by Hille Ris Lambers (1950) implies obligatory movement imposed by climate or other factors. Since a number of migratory aphids can survive on protected hosts in areas where the primary host also harbors the overwintering eggs, the extent of the obligation becomes difficult to determine. The best criterion for this and related groups of aphids is the production of sexuales on two host-species groups, which in most cases belong to separate plant families. Sexuales of *A. gossypii* have not yet been reported from any of the secondary hosts.

This pattern of alternation of hosts not only within a single family of plants, but also between two separate families of plants helps to complete the expected possible host relationships that could produce patterns of migration as they are observed in other aphids. Mordvilko (1928) predicted such "facultative" migration as described here.

If the aestivating form of the aphid should disappear, the life cycle on the primary host would be broken. Then the species would have to reinfest the primary host each fall to assure survival. Migration would then be obligatory and the necessary specialization of the sexual forms could easily follow. The males could be produced on secondary hosts and any females produced on the secondary hosts might eventually disappear when the eggs failed to survive the winter on the annual secondary host. Mordvilko (1928) postulates this as explanation for the more complicated types of life cycles found in the family Aphidae. Isolated groups on secondary hosts more favorable for winter survival might form new species. *Aphis sedi* (Kalt.), which lives only on *Sedum*, may have developed from *A. gossypii* Glover by such isolation.

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MORPHOLOGY OF THE REPRODUCTIVE SYSTEMS OF THE COTTON BOLL WEEVIL (COLEOPTERA, CURCULIONIDAE)[1]

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ABSTRACT

The genitalia and reproductive organs of the reproducing male and female cotton boll weevil, *Anthonomus grandis* Boheman, are described and illustrated. Descriptions are given of the musculature associated with the reproductive systems of both sexes.

The biology and control of the cotton boll weevil, *Anthonomus grandis* Boheman, have been studied rather extensively for approximately 60 years; however, little is known about the internal morphology of this important pest. Since the discovery by workers in Louisiana that the boll weevil undergoes diapause (Brazzel and Newsom, in press), there has been considerable interest in the conditions of the reproductive organs of this species as criteria for distinguishing diapausing from nondiapausing weevils. Brazzel and Newsom (in press) present photographs comparing the size and shape of the reproductive organs of the nondiapausing male and female boll weevils with those of weevils in a state of diapause. The object of the present study is to describe in detail the reproductive systems of both sexes of the reproducing (nondiapausing) weevil.

The majority of the literature pertinent to this subject has been reviewed by Bissel (1937), Schoof (1942) and Bruhn (1947). Little information has been published on the reproductive systems of weevils since the work of Bruhn (1947) on the male genitalia of 47 species of Rhynchophora. Khan (1949) made a comparative study of the internal and external morphology, including the reproductive systems, of both sexes of the rice weevil, *Sitophilus oryza* (Linnaeus), and the granary weevil, *Sitophilus granarius* (Linnaeus).

MATERIALS AND METHODS

Most of the weevils used in this study were collected as larvae and pupae in cotton squares (flower buds) near San Manuel, Mexico, during January and February 1958. After emergence from these squares at College Station, Texas, the adults were confined to cages and fed on cotton seedlings until needed for study. Since weevils from Mexico were available when this work was initiated in January 1958, they were used instead of weevils from Texas which were in short supply during that season. However, for comparative purposes some weevils from cultures maintained at College Station were studied. These were progeny of adults originally collected in the vicinity of College Station.

In preparation for fixation the weevils were first killed with cyanide. Immediately after death, the elytra and metathoracic wings were pulled off with a pair of forceps. A longitudinal slit was made down the middorsal line of the abdomen, and the insects were placed in a fixative consisting of 5 ml. of 40 percent formaldehyde, 2.5 ml. of glacial acetic acid, and 20 gms. of chloral hydrate, mixed together and diluted to 100 ml. with distilled water (Weaver and Thomas 1956). The weevils were left in the fixative for 4 to 12 hours, then were removed and dissected. Treatment for such a short period proved quite satisfactory, as the fat bodies and trachea were sufficiently hardened for easy removal, while the reproductive organs and muscles remained pliable enough to withstand considerable manipulation without breaking. Only a negligible amount of shrinkage of the soft tissues resulted from this treatment. Some fresh material was dissected also to examine structures that were not evident in the fixed specimens. These dissections were done in a physiological saline solution.

The terminology employed in the description of the reproductive systems of both sexes of the boll weevil is essentially that of Snodgrass (1935, 1957). For structures which Snodgrass did not consider, or where his terminology was inapplicable, terms used by various other authors were adopted (Sharp and Muir 1912, Sharp 1918, Tanner 1927 and Bissel 1937). For reference purposes the genital muscles of the boll weevil are designated here by numbers.

MALE REPRODUCTIVE ORGANS

The reproductive organs of the male boll weevil consist of a pair of testes with associated ducts and glands. A testis (fig. 1, Tes) lies in each side of the abdomen at about the level of the first, second, and third visible sterna. These are actually the third, fourth, and fifth sterna, since the first two are incorporated into the posterior portion of the metacoxal cavities and are not distinguishable as true sterna. Each testis is divided into two separate disk-shaped lobes. Each lobe is scalloped around the edge and is

[1]Technical contribution No. 3042, Texas Agricultural Experiment Station in cooperation with Entomology Research Branch, U. S. Department of Agriculture. Accepted for publication October 8, 1958.

further divided by septa into 10 or 11 wedge-shaped testicular follicles. These divisions are distinct in the young weevil but are more difficult to distinguish when the weevil ages and the lobes become distended with sperm.

A narrow duct arises from the inside center of each lobe of the testes (fig. 1). The two ducts from the same testis unite to form a larger duct. The length of these divergent ducts of the vas deferens (fig. 1, VD) depends upon the age and reproductive status of the weevil. They are somewhat longer in the old male than in the young one. A short distance below the union of the divergent ducts the vas deferens enlarges to form a club-shaped seminal vesicle (fig. 1, SV). The distinctness of this structure is also dependent upon the stage of sexual maturity of the weevil. It is scarcely distinguishable from the remainder of the vas deferens in the young male, but becomes considerably distended and chalky white when filled with sperm in an actively reproducing individual. The seminal vesicles of the pecan weevil, *Curculio caryae* (Horn), as reported by Bissel (1937), consist of distended areas of the ducts immediately below and contiguous to the basal ends of the accessory glands. Such enlargements are also present in the same position on the ducts of the boll weevil. The seminal vesicles of the boll weevil correspond in position and form to those described by Khan (1949) in the rice and granary weevils.

The accessory glands (fig. 1, AcGl) of the boll weevil consist of a pair of tubular diverticula arising from the sides of each vas deferens at the lower end of the seminal vesicle. There is considerable variation in the length and diameter of these glands. They become somewhat distended during periods of active secretion. The maximum length noted for a single gland was 5 mm. The accessory glands of the boll weevil are similar to those reported in the pecan weevil (Bissel 1937) and the apple-blossom weevil, *Anthonomus pomorum* Linnaeus (Miles 1923).

A short distance below the basal ends of the accessory glands the ducts from the testes unite to form the unpaired ejaculatory duct (fig. 1, EjD). The ejaculatory duct extends dorsally and decreases abruptly in diameter before entering the muscular sheath (figs. 1, 3, MS) between the apices of the aedeagal apodemes. This coiled duct extends posteriorly through the muscular sheath to open as the gonopore (fig. 3, Gpr) in the distal end of the sheath.

MALE GENITALIA

Sharp and Muir (1912) included a few curculionids in their study of the male genitalia of many species of Coleoptera. Sharp (1918) discussed various structures of the male genitalia of some Rhynchophora. The most comprehensive study of the male genitalia of weevils was made by Bruhn (1947). Several authors have investigated the genitalia of members of a genus or a higher category from the standpoint of taxonomic discrimination of species (Hopkins 1911, Barber 1935, Schoof 1942, Tanner 1943 and Davis 1947).

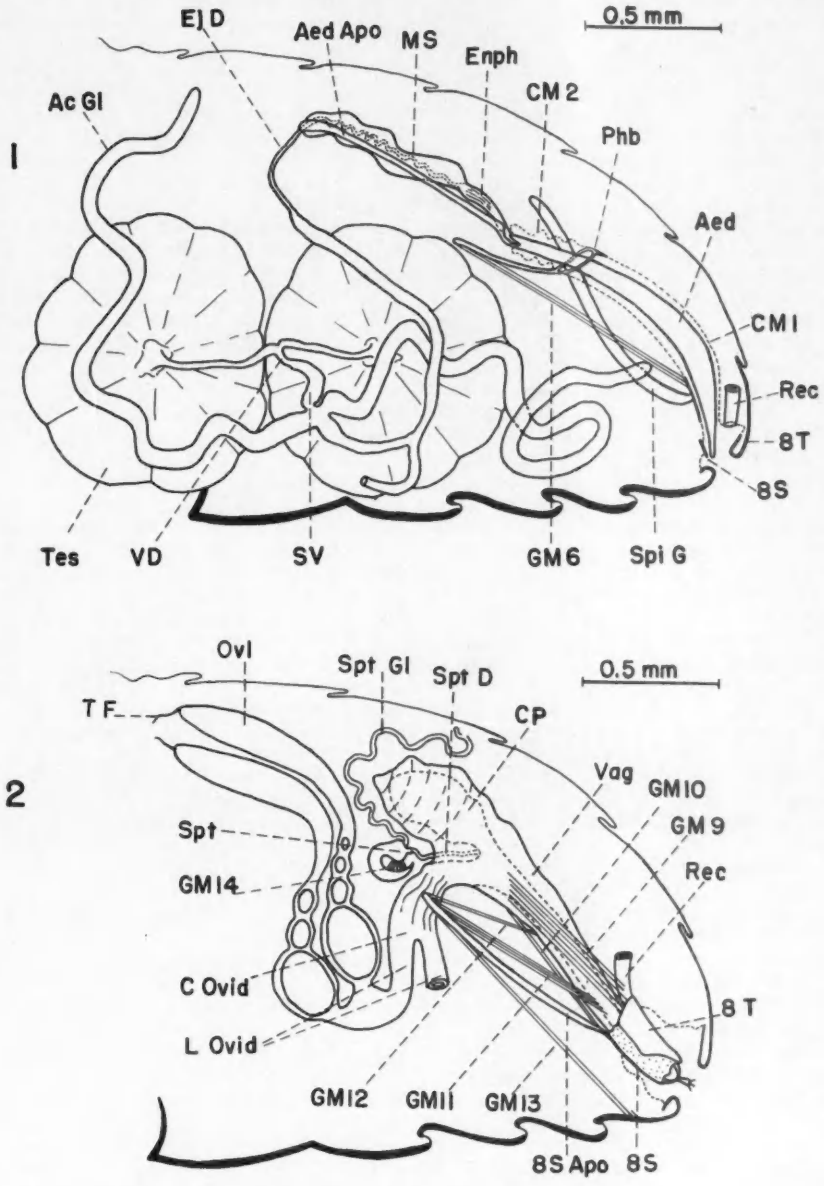
The genitalia, or phallic organs, of the male boll weevil include the aedeagus, endophallus, a muscular sheath enclosing the posterior end of the ejaculatory duct, a pair of aedeagal apodemes, a spiculum gastrale, and the two membranes enclosing the aedeagus. Associated with these structures are several muscles which serve as protractors and retractors of the aedeagus during copulation. Retractors of the endophallus are also present.

The aedeagus (figs. 1, 3, Aed) of the boll weevil is a somewhat flattened, sclerotized tube which, in repose in the abdomen, lies enclosed within the first and second connecting membranes (fig. 1, CM 1, CM 2). This structure, with the enclosed membranous endophallus, is exserted during copulation and transfers sperm from the male to the copulatory pouch of the female. To facilitate description the aedeagus is divided here into two portions, the body and the apex. The body is the tubular portion in which most of the endophallus is enclosed; the apex is the expanded, shovel-like tip distal to the posterior opening of the endophallus, or phallotreme (fig. 3, Phtr). The dorsolateral edges of the aedeagal body and apex are densely sclerotized, while the median ventral aspects are membranous and only slightly sclerotized. A dorsal membrane (fig. 3, DM), extending for the entire length of the body of the aedeagus, completes the tube in which the endophallus is contained.

A pair of aedeagal apodemes (figs. 1, 3, AedApo) extend from the base of the aedeagus anteriorly to about the level of the posterior margin of the

LIST OF ABBREVIATIONS

AcGl, accessory gland; *Aed*, aedeagus; *AedApo*, aedeagal apodeme; *An*, anus; *CM 1*, first connecting membrane; *CM 2*, second connecting membrane; *COvid*, common oviduct; *Cx*, coxite; *CP*, copulatory pouch; *DM*, dorsal membrane; *EjD*, ejaculatory duct; *Enph*, endophallus; *Epm*, epimere; *Ft*, foretube; *Gpr*, gonopore; *GM 1-GM 14*, inclusive, genital muscles; *LOvid*, lateral oviduct; *MS*, muscular sheath; *Ovl*, ovariole; *Phb*, phallobase; *Phtr*, phallotreme; *Rec*, rectum; *SpiG*, spiculum gastrale; *Spt*, spermatheca; *SptD*, spermathecal duct; *SptGl*, spermathecal gland; *Sty*, stylus; *SV*, seminal vesicle; *Tes*, testis; *TF*, terminal filament; *Vag*, vagina; *VD*, vas deferens; *Vu*, vulva; *7S*, seventh sternite; *7T*, seventh tergite; *8S*, eighth sternite; *8SApo*, apodeme of eighth sternite; *8T*, eighth tergite.



EXPLANATION OF PLATE I

FIG. 1.—Lateral view of male reproductive system with the right testis moved forward from normal position. Left testis, pair of accessory glands and vas deferens omitted. Musculature, except muscle GM 6, omitted.

FIG. 2.—Lateral view of female reproductive system in normal position in abdomen. Left ovary omitted. Left muscle only of paired muscles GM 9, GM 11 and GM 13 shown.

third tergite. The muscles directly involved with the protraction of the aedeagus are attached to the apices of these sclerotized rods. These apodemes of the boll weevil are essentially like those described in other species of weevils. Sharp (1918) states that all Rhynchophora, except *Platypus*, possess a pair of apodemes although they are very short in some species.

A prominent muscular sheath (figs. 1, 3, MS) attaches between the apices of the aedeagal apodemes and extends posteriorly to a point just short of the base of the aedeagus. The sheath is continuous at its posterior end with the membranous endophallus. The coiled ejaculatory duct can easily be traced through the full length of the muscular sheath but the opening of this duct, the gonopore, at the posterior end of the sheath is difficult to distinguish. Although the muscular sheath is usually short in dissected weevils, it must be considerably extended during copulation when the gonopore is moved posteriorly to a point near the tip of the aedeagus.

A short portion of the anterior end of the endophallus (fig. 3, Enph) consists of a somewhat transparent, membranous sac. Distad of this area, the endophallus enlarges and enters the cavity of the aedeagus. At its posterior end it becomes smaller and the edges turn outward and backward to attach to the aedeagus. The opening of the endophallus at this point is termed the phallotreme (fig. 3, Phtr). The inner wall of the endophallus, from the posterior margin of the clear, membranous area to the phallotreme, is rather uniformly covered with small, sclerotized spines. When the endophallus is retracted into the aedeagus, the apices of these spines point posteriorly, but when the endophallus evaginates during copulation the spines become external and reverse their direction to point toward the base of the aedeagus (fig. 7). The evagination of the endophallus serves a twofold purpose: (1) the gonopore is moved posteriorly to near the tip of the aedeagus, from which point the sperm are discharged from the ejaculatory duct; and (2) the anteriorly projecting spines probably serve to anchor the aedeagus and endophallus in the vagina of the female during copulation. When evaginated the endophallus forms a cylindrical, double-walled expansion above the apex of the aedeagus (fig. 7). Complete evagination of the tube was not observed although partial evagination was noted several times. Assuming that the entire spine-bearing portion of the tube becomes external during complete evagination, the endophallus would project about 0.4 mm. past the tip of the aedeagus. The various lobes described on the evaginated endophallus of other weevils (Sharp 1918 and 1920, Barber 1935, and Schoof 1942) are not present in the boll weevil. This insect also lacks structures (transfer apparatus) associated with the gonopore and various plates present within the endophallus described in several other species. Apparently such sclerotized structures serve to effect a close connection between the gonopore of the male and the opening of the spermathecal duct of the female. The absence of these specialized structures in the male boll weevil indicates that the sperm are not introduced directly into the spermathecal duct in this species, but must gain entrance in some other manner. Apparently, during copulation the posterior end of the evaginated endophallus either enters or fits closely against the opening of the copulatory pouch. From this point the sperm are discharged into the pouch and later move into the spermathecal duct. After copulation, the copulatory pouch as well as the spermatheca of the female usually contains a large amount of sperm.

The phallobase (figs. 1, 4, Phb) of the boll weevil is composed of a thin, sclerotized ring bearing an anteriorly projecting apodeme on its ventral side. A pair of thin epimeres (fig. 4, Epm) project posteriorly from the dorsal side of the ring. In the normal position, the ring of the phallobase encircles the aedeagus about one-third of the distance from the base. The muscles directly involved in the protraction and retraction of the aedeagus are attached to the ring of the phallobase or to the ventral apodeme.

The spiculum gastrale (figs. 1, 4, SpiG) is composed of a prominent rod arising from a lightly sclerotized base beneath the apical portion of the aedeagus. The anterior and posterior margins of the thin base plate are often difficult to distinguish from the first connecting membrane with which the base is continuous. The heavily sclerotized rod extends anteriorly and dextrad from the center of the base plate to lie with its apex alongside of and slightly higher than the base of the aedeagus. Two muscles connect the apex of the rod with the phallobase.

In repose the aedeagus is enclosed within the first and second connecting membranes. The first connecting membrane (fig. 1, CM 1) originates from the body wall and extends anteriorly as a tube around the aedeagus to attach to the ring of the phallobase. The rectum (fig. 1, Rec) enters the dorsal aspect of this membrane near the body wall. Ventrally, the membrane connects the base of the spiculum gastrale and the eighth sternite (fig. 1, 8S) to the body wall.

The second connecting membrane (fig. 1, CM 2) passes anteriorly from the ring of the phallobase to connect to the base of the aedeagus. The dorsal portion of this membrane is continuous with the dorsal membrane of the aedeagus.

The genital muscles of male curculionids have received less attention than any of the other structures of the reproductive system. Bissel (1937) described in some detail the genital muscles of the pecan weevil. The muscles associated with the genitalia of the plum curculio, *Conotrachelus nenuphar* (Herbst), were investigated by

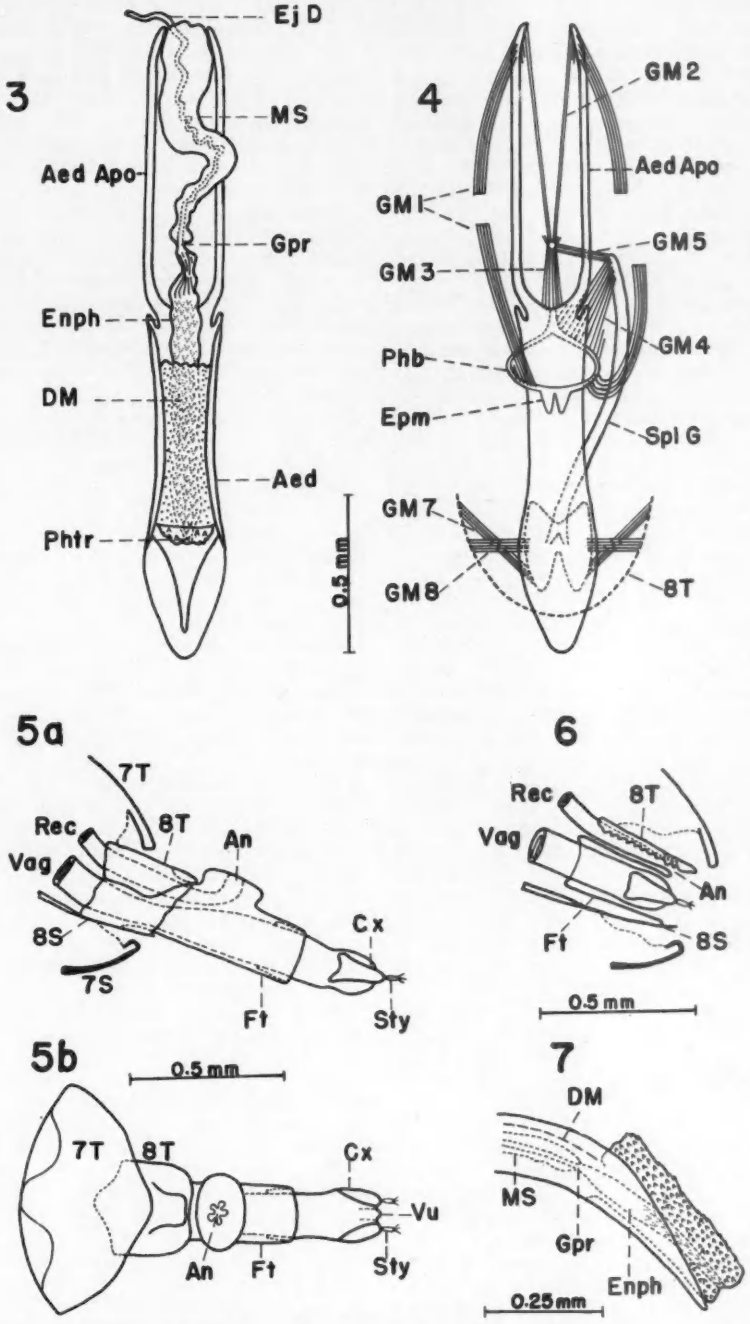


FIG. 3.—Dorsal view of aedeagus and aedeagal apodemes showing the muscular sheath and endophallus.
FIG. 4.—Dorsal view of male phallic organs showing associated musculature, except muscle GM 6.
FIG. 5a.—Lateral view of exserted ovipositor.
FIG. 5b.—Dorsal view of same.
FIG. 6.—Lateral view of apex of female abdomen showing the retracted ovipositor.
FIG. 7.—Apex of aedeagus showing the partially evaginated endophallus.

Schoof (1942). Others (Hopkins 1911, Miles 1923, and Munro 1914) have contributed some information on this subject.

The muscles associated with the phallic organs of the boll weevil, with one exception, consist of narrow bands which are a few to several fibers in width and a single fiber in thickness. The exception to this type is a short, stout muscle connecting the apex of the spiculum gastrale with the phallobase.

The retractors of the endophallus (not shown in illustrations) consist of a pair of muscles, each of which originates from the inner side of the apex of an aedeagal apodeme and extends posteriorly to insert on the muscular sheath and endophallus. Some of the fibers of this pair of muscles attach near the posterior end of the muscular sheath while others are longer and attach at various points along the basal half of the endophallus.

A pair of longitudinal muscles (fig. 4, GM 1) originates from the dorsolateral aspects of the ring of the phallobase and passes anteriorly to insert on the apices of the aedeagal apodemes. Ventrally, another pair of muscles (fig. 4, GM 2) diverges anteriorly from a common origin on the apex of the apodeme of the phallobase to insert on the apices of the aedeagal apodemes. These two pairs of muscles serve as protractors of the aedeagus. The aedeagal retractor consists of a short muscle (fig. 4, GM 3) extending dorsally and posteriorly from the apex of the ventral apodeme to the base of the aedeagus.

The most prominent one of the two muscles originating from the apex of the spiculum gastrale is a thick, fan-shaped muscle (fig. 4, GM 4) which inserts along the lateral and ventral aspects of the right side of the phallobase ring. Fibers of this phallobase retractor frequently extend for some distance along the ventral apodeme. A much less distinct muscle (fig. 4, GM 5) connects the apex of the spiculum gastrale with the apex of the ventral apodeme. This muscle, which probably also acts as a phallobase retractor, is difficult to distinguish when the larger muscle (GM 4) extends onto the ventral apodeme. In this case the two often appear as a single wide muscle.

A wide muscle (fig. 1, GM 6) originates from the anterior margin of the base of the spiculum gastrale and passes forward to insert along the apodeme of the phallobase. When this muscle contracts, it moves the phallobase posteriorly to allow full extension of the aedeagus.

The only genital muscles which attach to the body wall are two pairs of suspensory muscles which connect the base of the spiculum gastrale to the lateral edges of the eighth tergite. The oblique suspensors (fig. 4, GM 7) consist of fewer but heavier fibers than the lateral suspensors (fig. 4, GM 8). These muscles stabilize the phallic organs within the abdomen.

FEMALE REPRODUCTIVE ORGANS

The female reproductive organs of the cotton boll weevil are similar to those reported for other species of weevils. The boll weevil possesses a pair of ovarioles (fig. 2, Ovl), constituting an ovary, in each side of the abdomen. The size of the ovarioles varies with the age and reproductive status of the weevil.

Extending forward from the apex of each ovariole is a slender terminal filament (fig. 2, TF) which unites with that of the adjacent ovariole to form a threadlike suspensory ligament. The suspensory ligaments pass forward and appear to attach dorsally in the anterior region of the abdomen. The anterior ends of the two ovaries converge toward the center of the body just above the alimentary canal.

Each pair of ovarioles opens into the widened anterior end, or calyx, of a lateral oviduct (fig. 2, LOvid). Shortly distad to this point, the paired lateral oviducts curve upward and unite to form the common oviduct (fig. 2, COvid). The common oviduct is largely membranous and is slightly darker in color than either the lateral oviducts or the vagina. It opens into the ventral side of the vagina immediately behind the posterior end of the expanded copulatory pouch.

The vagina (fig. 2, Vag) is a long, muscular tube extending anteriorly from within a vestibule formed by the eighth tergite and eighth sternite. At its anterior end, it is expanded into a large, muscular, copulatory pouch (fig. 2, CP), or bursa copulatrix. The dotted line (fig. 2) shown within the copulatory pouch and vagina represents the inner wall of these two structures.

A prominent C-shaped spermatheca (fig. 2, Spt), consisting of an outer sclerotized wall enclosing a membranous sac, lies beneath the copulatory pouch. A slender spermathecal duct (fig. 2, SptD) extends from the end of the enlarged portion of the spermatheca and enters the muscular tissue at the junction of the copulatory pouch and common oviduct. This duct extends through the tissue for a short distance to open into the interior of the vagina. The sperm enter and leave the spermatheca through this duct.

The long spermathecal gland (fig. 2, SptGl) opens into the spermatheca near the entrance of the spermathecal duct. This tubular gland, which often measures up to 2 mm. in length, lies coiled about in the abdomen. Such a long, slender gland is apparently unusual among the curculionids, as in studies on other species (Tanner 1943, Munro 1914, Bissel 1937, and Miles 1923) this gland has been described as being sac-like and rather short.

The genital muscles of the female boll weevil, like those of the male, have received little study. The genital muscles of the pecan weevil were mentioned by Bissel (1937). Henneguy (1904) figured the genital muscles of the apple-blossom weevil.

In structure the genital muscles of the female boll weevil resemble those of the male. They consist of bands, each of which is made up of a few fibers.

A wide muscle (fig. 2, GM 9) passes forward from each lateral edge of the eighth tergite (fig. 2, 8T) and is inserted on the side of the vagina just posterior to the entrance of the common oviduct. A few fibers of this pair of muscles also originate on the sides of the rectum immediately anterior to the point where it enters the vestibule beneath the eighth tergite.

An unpaired muscle (fig. 2, GM 10) originates from the anterior edge of the eighth sternite and extends forward to insert on the underside of the vagina posterior to the common oviduct.

The paired dorsal muscles (GM 9) and the unpaired ventral muscle (GM 10) serve to shorten the vagina during copulation so that the evaginated endophallus of the male is able to reach the opening of the female copulatory pouch. The contraction of these muscles probably also aids in the movement of the egg down the vagina during oviposition.

A pair of muscles and an unpaired one originate from the apex of the apodeme of the eighth sternite (fig. 2, 8SApo). The two muscles of the paired set (fig. 2, GM 11) diverge posteriorly from the apex of the apodeme and insert on the sides of the vagina near where it enters beneath the eighth tergite. These muscles act as retractors of the ovipositor. The unpaired vaginal retractor muscle (fig. 2, GM 12) extends posteriorly from the apex of the apodeme and inserts on the ventral side of the vagina.

A rather indistinct muscle (fig. 2, GM 13) arises from each lateral edge of the floor of the seventh sternite, and the pair extend dorsally and anteriorly to converge on the apex of the eighth sternal apodeme. These muscles probably act as depressors of the apodeme.

The genital muscles which connect the anterolateral edges of the eighth tergite with the sides of the seventh tergite are not illustrated. These muscles serve to stabilize the genitalia within the abdomen.

The spermathecal compressor muscle (fig. 2, GM 14) contracts to force sperm out of the spermatheca and up through the duct into the vagina.

FEMALE GENITALIA

In a study of the female genitalia of Coleoptera, Tanner (1927) included five species of curculionids, four of which were illustrated. Tanner (1943) later used the form of the sclerotized terminal plates of the ovipositor as aids in the identification of several species of weevils of the subtribe Hydronomi. Davis (1947) similarly employed these structures in a taxonomic investigation of weevils of the tribe Ophryastini. Bissel (1937) thoroughly investigated the structure of the long ovipositor of the pecan weevil and the method by which it is retracted and folded within the abdomen. The sclerotized terminal structures of the ovipositors of the rice and granary weevils were studied by Khan (1949).

The retracted ovipositor of the female boll weevil is contained within a cavity formed by the eighth tergite and eighth sternite in the posterior end of the abdomen. The eighth tergite (figs. 5a, 5b, 8T) is a somewhat saddle-shaped structure which is densely sclerotized along the edges and less sclerotized in the middle. The eighth sternite (figs. 5a, 6, 8S), with its anteriorly projecting apodeme, lies beneath the eighth tergite. This sternite is connected by membranous tissue and muscle fibers to the lateral edges of the dorsal eighth tergite, thus forming the vestibule into which the rectum and vagina enter. The vestibule is attached to the terminal abdominal segment by a membrane (fig. 2, dotted line). When the ovipositor is exserted, the eighth tergite and sternite spread slightly apart and project for a short distance outside of the abdomen (figs. 5a, 5b).

When retracted into the vestibule, the ovipositor forms a double-walled tube with the membranous foretube (fig. 6). The foretube is continuous with the membrane around the anus and, therefore, when it evaginates and becomes external during the exsertion of the ovipositor the opening of the alimentary canal is also moved posteriorly. In the forceful exsertion of the ovipositor, the anus moves out from under the eighth tergite and opens to the exterior in the center of a dorsal expansion of the foretube (figs. 5a, 5b). However, in normal oviposition the ovipositor is probably not so fully exserted and the anus does not become external.

The relationship of the structures within the vestibule when the ovipositor of the boll weevil is retracted is essentially the same that Bissel (1937) reported in the pecan weevil. In the pecan weevil, however, the retraction and storage of the ovipositor is more complicated due to extreme length of that structure.

A partially sclerotized coxite (figs. 5a, 5b, Cx) is borne on each side of the end of the ovipositor. Projecting from the apex of each of these coxites is a fingerlike stylus (figs. 5a, 5b, Sty) which bears a few setae at its tip. The external aperture, or vulva (fig. 5b, Vu), of the reproductive system opens between the coxites at the distal end of the ovipositor.

ACKNOWLEDGMENTS

The author gratefully acknowledges the helpful advice given by Dr. D. R. King in connection with this investigation. Thanks are also due several other members of the Department of Entomology, The A. & M. College of Texas, who read and constructively criticized the manuscript.

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THE EFFECTS OF FEEDING ANTIMITOTIC SUBSTANCES TO ADULT FEMALE HABROBRACON (MICROBRACON HEBETOR (SAY); HYMENOPTERA, BRACONIDAE)[1, 2]

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ABSTRACT

Except at an extreme dilution of 0.0005%, colchicine proved toxic to adult Habrobracon and to trophocyte-oocyte units. Oviposition and hatchability records are presented. With 0.0005% colchicine, a compensatory type of oviposition curve was obtained in which eggs laid late in life nearly compensated for a lag during young adulthood. Completely compensatory oviposition was obtained by feeding 0.8% heparin. Egg hatchability exceeded control values significantly for the come pensatory period not only for this, but also for lower heparin dosages. These results differ from those obtained with enzyme inhibitors or antimetabolites. Altered protoplasmic viscosity is favored in explanation.

Although the chemical inhibition of fertility is being carefully explored in mammals, surprisingly little work has been done with insects except in the field of ovicides. Investigations on gonads have tended to be histochemical, and directed toward the ovaries. An excellent review by Bonhag (1958) covers this area.

Recently, Mitlin et al. (1957) showed that ovarian development in adult house flies can be prevented by feeding colchicine, nitrogen mustard, or aminopterin. The fertility of male flies was unaffected by this heterogeneous selection of substances. Any cyto-inhibitive substance, regardless of its mode of operation, and provided it reaches the site of action intact, may have opportunity to act during the progressive series of ovarian changes occurring in the 3 days of adulthood necessary for the achievement of sexual maturity by female house flies.

The same three substances and additional compounds from each class have been fed to adult female Habrobracon. Ovarioles here are mature upon emergence from the cocoon, and being in the functional state supply a sequential arrange-

[1]This document is based on work performed under Contract AT-(40-1)-1314 for the U. S. Atomic Energy Commission. Howard E. Erdman and Stephen J. Karakashian provided helpful technical assistance.

[2]Contribution from the North Carolina Agricultural Experiment Station. Published with the approval of the Director as Paper No. 896 of the Journal Series. Accepted for publication October 13, 1958.

ment of cell types which should enable a determination of relative susceptibilities to treatment. The present report concerns results with colchicine and heparin, the only two substances fed to date which have altered the pattern of fecundity in a similar way. Other potent substances have induced their own peculiar pattern and will be treated in subsequent publications. Impotent substances include ovarian extracts from other phyla and queen bee substance. These compounds also were ineffective in halting the growth of house fly ovaries (Mitlin and Baroody 1958).

Daily egg production, hatchability of the eggs, and microscopic examination of dissected ovarioles are compared with suitable controls. Life span was taken as a measure of general toxicity.

MATERIALS AND METHODS

The Habrobracon (*Microbracon hebetor* (Say)) were from wild type Whiting stock number 33. Adult females were dissected from cocoons and starved until a dorsoventral flattening of abdomens gave visible evidence of a depleted fat body. A droplet of food mixture was then deposited in each holding vial, whereupon wasps would feed unless the mixture was unpalatable. The average wasp eats a meal of 0.49 mm^3 determined by the volume of its distended crop (Grosch and Sullivan 1952). Only one meal was allowed in present experiments.

Amorphous colchicine (Fisher Scientific Company) added to sugar solutions proved relatively unpalatable, judging from refusal at concentrations greater than 0.01 percent. Forty-one females were fed this solution. Twenty supplied oviposition and hatchability data. The remainder were dissected three per day for the week following ingestion. Additional graded dilutions of colchicine in sugar solution were fed until no shortening of life span resulted. This level was not reached until 0.0005 percent mixtures were fed.

The heparin mixtures were prepared by dissolving 0.1 gm of sodium heparinate (Upjohn Company) in 10 ml. of distilled water. Portions of this solution were further diluted by adding a saturated solution of commercial granulated sugar to make up 0.8, 0.7, 0.5, and 0.1 percent mixtures. The most dilute mixture is a heparin level employed by cell physiologists (Heilbrunn and Wilson 1949). We are indebted to Dr. L. V. Heilbrunn and Dr. W. L. Wilson for the use of heparin they had demonstrated to be effective in the delay of cleavage of marine eggs. Without difficulty, samples of 20 females were fed each heparin mixture immediately after preparation. An additional eight females were fed the highest dose and dissected during the following 3 days for examination of their ovaries.

Each female was held in an individual stender dish, 20 x 40 mm., with two host caterpillars. On each successive day the more flaccid caterpillar was replaced at the time of egg collection. Collected eggs were immersed in mineral oil, an empirical method for obtaining the best hatchability records. The incubation temperature for eggs, as well as for females producing them, was 30° C. The controls run for colchicine and heparin experiments, respectively, were fed sugar solution.

RESULTS

Life Span.—The mean life span for wasps fed 0.01 percent colchicine was a short 10.21 ± 1.76 days, which is to be compared with a control mean life span of 25.66 ± 1.45 days. Improvement in life span occurred only when the colchicine

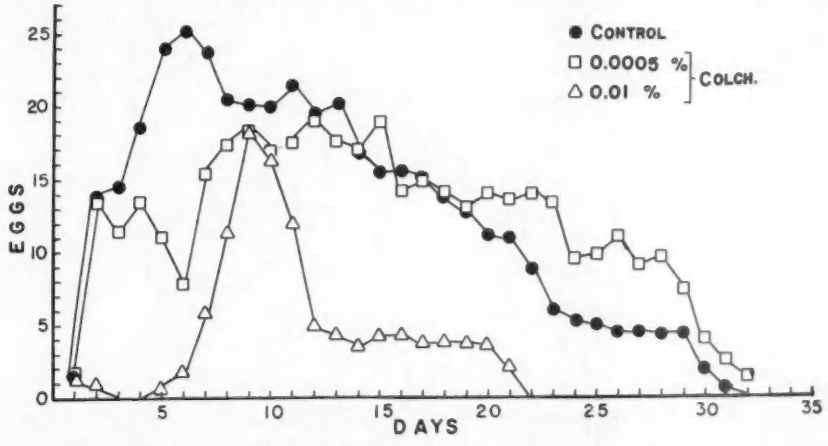

FIG. 1.—A comparison with control values of the average number of eggs deposited by Habrobracon after (a) ingesting a very small amount of colchicine in a sugar mixture, and (b) ingesting the highest concentration of colchicine found palatable.

was diluted to 0.0005 percent. The mean life span then was 26.00±2.27 days. In the 0.005 to 0.001 percent range, survival was no better than after 0.01 percent feedings.

In contrast, heparin feeding did not alter life span significantly. After the highest heparin feeding, females lived 23.66±1.62 days. The mean life span for controls was 24.27±1.58 days. Survival after other heparin feedings varied less than ±2 days from the control mean.

Fecundity.—Figure 1 compares the daily oviposition of wasps fed the lowest and highest colchicine mixtures with control records. Intermediate concentrations of colchicine have provided curves which fit between those experimental results shown. They are omitted for the sake of clarity of the figure.

The 0.01 percent feeding of colchicine is characterized by a prompt decline to infecundity followed soon by a short-lived surge which failed to achieve control values. Egg production after the low feeding, 0.0005 percent, not only achieved control values after a slow climb, but ultimately exceeded them. In total number of eggs produced, this pattern results in an average per female of 392.0 eggs as compared to 399.1 eggs per control female. Therefore eggs deposited late in life have nearly compensated for the lag during the first half of life.

Figure 2 presents oviposition after the highest heparin feeding (0.8 percent) plotted along with control records. Even more impressive compensation in egg deposits is shown by a reduction of the peak production of youth and a moderation in the decline of senility. In this experiment the same number of eggs were laid as by controls, merely in a different pattern. Heparin-fed wasps averaged 294.0 eggs per female while controls averaged 294.3 eggs in the 21-day period shown. Lifetime averages were 325.8 and 325.4, respectively.

The 0.1 percent curve, which does not differ significantly from that of the control, and the family of curves resulting from the intermediate feedings are omitted for the sake of clarity of the figure.

In controls, eggs laid during successive weeks are derived from cells differing morphologically and physiologically at the time when an experiment is begun, i.e. at the time of experimental treatment. Those deposited the first week were oocytes accompanied by differentiated nurse cells, those appearing the third week derived from oogonia visibly undifferentiated on the initial day (Whiting 1940). Eggs laid the second week were in the transitional stage involving cell multiplication and differentiation during the first day. The transitional cells would be expected to show the greatest susceptibility to mitotic inhibitors which influence the spindle. If pressure from the proliferative region contributes to the time course of oviposition, a passive basis for the early leveling in the heparin curve is supplied. On the other hand, colchicine has a toxic effect upon oocytes when supplied in appreciable concentration.

Hatchability.—Hatchability is summarized in tables 1 and 2 from the standpoint of control ovariole histology. Hatchability normally varies around levels which reflect the several different cell types present at the time of treatment as given above.

In general, colchicine influenced hatchability adversely (table 1). Except for the lowest dose, hatchability was poor for the first week, and although better results were obtained subsequently, hatchability was generally lower than controls. On the other hand, an unexpected result was the manner in which hatchability held up in the eggs laid during old age of the wasps fed the 0.0005 percent colchicine mixture.

Similar but even more impressive was the hatchability of the eggs laid by heparin-fed

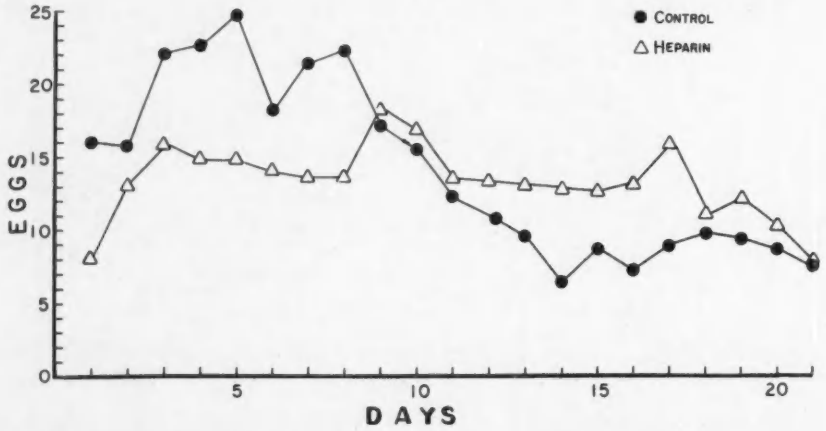

FIG. 2.—A comparison with control values of the average number of eggs deposited by Habrobracon fed 0.8% heparin in a sugar solution.

Table 1.—The percent of eggs which hatched. Means and standard errors for colchicine-fed females.

Colchicine Dose (%)	Days on which eggs were deposited			
	1–7	8–14	15–21	22–28
0.01	[a]	61.62±13.85	26.69± 4.71	
0.005	0	72.43±12.23	53.11±11.39	
0.0005	92.74±0.73	89.51± 0.66	77.84± 1.67	70.10±2.23
Controls	97.07±0.49	92.16± 0.91	76.39± 1.34	49.46±1.96

[a]0% on day 1; 66.7% on day 2, based on very few eggs; day 5 and 6, 60%.

females. Control hatchability was exceeded throughout the period of study. As shown in table 2, the divergence becomes progressively greater and is especially striking during old age. It should be realized however that in this set of experiments, few eggs were laid after the third week and these were deposited irregularly.

Histological observations.—Dissections of females fed higher colchicine doses revealed striking differences from control ovarioles. Distally ovarioles enlarged to two or three times the normal diameter early in the infecund period due to an accumulation of undifferentiated cells, presumably oogonia. The germarium enlarged first but by the third day, the vitellarium showed irregular enlargements along with partial degeneration of its contents. Instead of a single sequence of developing oocyte-trophocyte units, duplicate units lying side by side began to appear. By the fourth day much debris had accumulated near the calyx. Immediately above this degenerate mass there were empty spaces in the lumen of the egg tube. However, the picture soon changed, so that by the fifth day ovariole diameters were decreasing and the contents in about half of the ovarioles appeared qualitatively normal. Ovariole diameters were standard by the sixth day, and complete normality of histomorphology was achieved by the seventh.

After the lowest colchicine dose and after the highest heparin feeding, the only change observable upon dissection was a slight enlargement in diameter of the germarium region of ovarioles.

DISCUSSION

Contrasts between life span, egg production, and hatchability of the controls indicate that a more extreme stage of inanition had been reached by the females fed heparin. Not all the factors responsible are known. However, even though wasps are held in an incubator, it is difficult to eliminate completely mechanical and other stimuli which agitate females during the necessary period of starvation prior to feeding. In spite of this, a general similarity has emerged between the effects of feeding considerable doses of heparin and those of feeding very dilute colchicine.

The simplest explanation of the pattern of oviposition is that both agents influenced its time course through delayed cell division. Colchicine, a drug of plant origin, is the classic spindle inhibitor still considered the most specific and potent agent of its type (Eigsti 1957). Heparin, a mucopolysaccharide widely distributed in animals, delays cleavage of marine eggs (Heilbrunn and Wilson 1949), prevents the division of tumor cells (Goerner 1931; Heilbrunn 1956), and lowers mitotic activity of tissue cultures (Fischer 1936; Paff et al. 1952). There is no direct evidence that heparin as such gets through the wall of the braconid digestive tract, although parts of it are extremely thin-walled. Nevertheless something unusual reached the physiological interior, and subsequently the gonad, to produce the striking—and except for colchicine—unique alteration in the time course of egg deposit.

Although selective inhibition of enzymes by heparin has been suggested (Benditt 1957), and action as a general macroanionic inhibitor of enzyme systems has been postulated (Spensley and Rogers 1954), we favor interpretation of present results from the standpoint of modified protoplasmic viscosity (Heilbrunn 1956). Experiments with classic enzyme inhibitors and

Table 2.—The percent of eggs which hatched. Means and standard errors for heparin-fed females.

Heparin Dose (%)	Days on which eggs were deposited			
	1–7	8–14	15–21	22+
0.8	97.03±0.85	92.80±1.48	91.57±1.09	86.38±4.51
0.7	96.94±0.68	95.89±1.16	91.15±4.08	85.49±5.34
0.5	96.99±0.81	94.93±1.13	90.08±1.83	85.45±3.66
0.1	96.91±1.27	94.64±2.11	91.67±1.27	84.97±5.24
Controls	94.73±0.98	86.43±4.12	73.33±4.46	48.23±5.10

available antimetabolites have furnished modified oviposition records completely different from any presented above. Periods of high and low egg production following feedings of such substances are almost completely antithetic to present results.

At doses which would not be considered excessive for many organisms, the irreversible effects from colchicine obscured evidence of delayed cell division. Judging from the debris in dissected ovarioles, low egg production traces to cytotoxic consequences of a colchicine feeding. The prompt appearance of debris indicates that trophocyte-oocyte units are affected. During this phase of development the spindle is secondary in importance to elaborative and secretory processes. The very low tolerance of the adult was even more surprising, although it was known that animals do not tolerate colchicine concentrations much weaker than those used routinely on plants (Dermen 1940). Braconid adults are not vulnerable to disturbances of cell division since there are none outside of the gonial cells. Thus a toxic effect on the adult also suggests interference with a vital metabolic step.

Colchicine has been applied to many different organisms for diverse reasons and an immense bibliography has accumulated (Eigsti and Dustin 1955). Only one publication has direct pertinence. Inoba (1940) immersed 575 uneclosed braconid females in 0.05 percent aqueous colchicine. Most of the wasps survived the treatment but 85 percent of them failed to reproduce. Even the females he classified as fertile produced few offspring, although Inoba obtained enough material to answer his questions on sex determination. Unfortunately for present comparisons, Inoba's data were gathered from transfers made every 3 or 4 days rather than daily. Nevertheless, he obtained few offspring until his third transfer, that is, the ninth or twelfth days. This suggests a pattern exactly like that of figure 1.

Hatchability results are more difficult to interpret. Either a higher hatchability of eggs delayed from normal earlier deposits masks the senile decline, or the physiological conditions resulting in such a decline are alleviated. In particular, lethal accidents during chromosome duplication and segregation may be less frequent when division has slackened. Whatever the explanation, the heparin feedings were surprisingly beneficial in terms of reproductive potential. With no overall decrease in the number of eggs deposited, but with consistently higher hatchability than controls, more live larvae per mother resulted.

SUMMARY

Colchicine feedings at levels considered routine produced degenerative changes in the differentiated portion of ovarioles, and shortened adult life span. This indicates a main effect on something other than cell division. An altered pattern of oviposition traceable to the time course of cell division was obtained only with very dilute colchicine. On the other hand, relatively high concentrations of heparin gave a flattened, compensatory type of egg production curve. The hatchability after heparin and dilute colchicine feedings held up surprisingly well during old age in contrast with control values.

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SYSTEMATIC STUDY OF THE PUPAE OF THE OEDEMERIDAE (COLEOPTERA)[1]

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ABSTRACT

Pupae were studied of *Calopus angustus* LeC., *Nacerdes melanura* (L.), *Xanthochroa erythrocephala* (Germ.), *Ditylus quadricollis* (LeC.), *Alloxacis dorsalis* (Melsh.), *Oxycopis thoracica* (F.), *O. suturalis* (Horn), *Sessinia livida* (F.), and *Oedemera virescens* (L.). These nine species represent the three recognized oedemerid subfamilies and the three tribes of Oedemerinae. A key is given to these pupae, and a family diagnosis is based upon them. The pupae, like the larvae, seem to be of three major types, i.e., *Calopus*, *Oedemera*, and all others, with that of *Calopus* being most like pupae of related heteromerous families.

This preliminary systematic study of the pupae of the Oedemeridae comes as an outgrowth of a recent (though as yet unpublished) investigation of oedemerid larvae, in that the pupae employed here were associated with the larvae. These pupae represent the three subfamilies—Calopodinae, Nacerdinae, and Oedemerinae—recognized by Arnett (1951), as well as the three tribes of the Oedemerinae. The key presented herein shows the pronounced differences that exist between most species, but descriptions of each species are not given since only nine are dealt with, and some of these are known from only single specimens.

One of the specimens of *Oedemera virescens* (Linnaeus) was loaned by C. M. F. von Hayek of the British Museum (Natural History). All other pupae are in the collection of the U. S. National Museum.

A number of oedemerid pupae have been described and illustrated in the past (see annotations to references in Bibliography), but most of the accounts overlook the characters here regarded as having diagnostic value. These descriptions, therefore, are not incorporated in this paper.

Oedemerid pupae are pale, elongate, convex, and moderate-sized; they possess urogomphi, lack gin-traps, and bear a ventrally reflexed head. Since little is known concerning the pupae of the families of Coleoptera, it is not possible to list characters that will distinguish pupae of Oedemeridae from those of all other beetles. However, the following diagnosis should serve to separate oedemerid pupae from those of taxa believed to be closely related (Arnett 1951; Böving and Craighead 1931; Rozen, unpublished data).

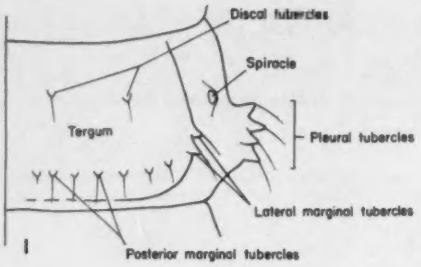
DIAGNOSIS OF THE PUPAE OF THE OEDEMERIDAE

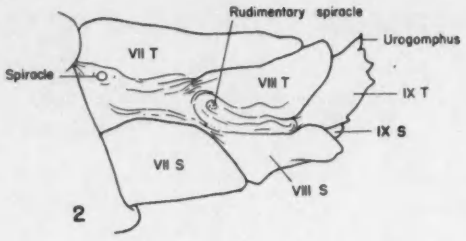
Setiferous tubercles moderately small, thus all tubercles of pronotum (figs. 18, 21, 26, 28) or of abdominal sterna less than one-tenth as long as greatest width of pronotum; NOT some setiferous tubercles on pronotum (*Cephaloon* sp. [Cephaloidae]) or on middle abdominal sterna (*Dendroides canadensis* Latreille, *concolor* (Newman), and *ephemeroides* (Mannerheim); *Schizotus cervicalis* Newman; and *Neopyrochroa femoralis* (LeConte) [all Pyrochroidae]) longer than one-fourth greatest width of pronotum. Setiferous tubercles of pronotum (figs. 6, 18, 21, 26, 28), except in *Calopus angustus*, weakly sclerotized, scarcely pigmented apically, not sharply pointed, and each with seta arising from apex; NOT setiferous tubercles of pronotum distinctly sclerotized, moderately pigmented, sharply pointed, and each with seta arising from a definitely subapical position (as in *Pytho americanus* [Pythidae], fig. 5, *Eurystethus debilis* (Mannerheim) [Eurystethidae], *Othnius umbrosus* LeConte [Othniidae], *Melandrya striata* Say [Melandryidae], and *Synchroa punctata* Newman [Synchroidae]). Pronotum(figs. 18, 21, 26, 28) with posterolateral angles not produced; NOT with posterolateral angles strongly produced (as in *Penthe* sp. [Melandryidae]). Elytra glabrous (figs. 14, 17); NOT with exterior surface beset with numerous fine, elongate setae (as in *Eurygenius campanulatus* LeConte [Pedilidae]). Abdominal terga 2 to 6 (figs. 1, 8, 10, 13, 16, 19, 23, 25, 27) with lateral extremities at most only slightly produced laterally, more or less in same plane as rest of tergum; NOT with lateral margins strongly produced upward and outward (as in *Synchroa punctata* Newman [Synchroidae]; *Serropalpus barbatus* (Schaller) [Melandryidae]; *Alobates* sp., *Zopherus haldemani* Horn, and *Bolitotherus cornutus* (Panzer) [all Tenebrionidae]).[3]

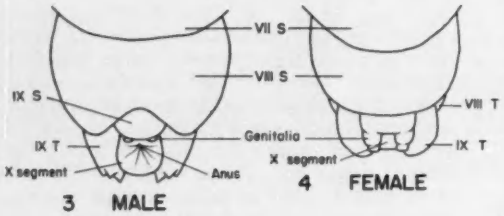
Calopus angustus agrees with the rest of the oedemerids except that many of the pronotal tubercles (as well as some of the abdominal ones) are somewhat sclerotized and have subapical setae. However, the following characters distinguish it from related nonoedemerid genera bearing similar tubercles: Fourth abdominal sternum with largest setiferous tubercle on each side small, less than one-half length of pleural tubercle (largest setiferous tubercle in *Pytho*

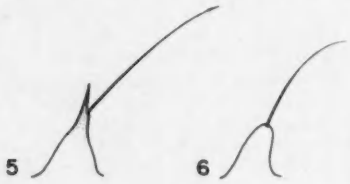
[1]Accepted for publication October 16, 1958.
[2]Present address: Department of Zoology and Entomology, The Ohio State University, Columbus 10.

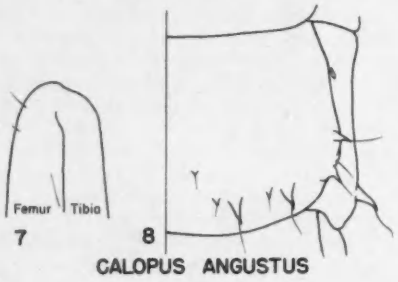
[3]This feature may be characteristic of all Tenebrionidae. See Daggy (1947).

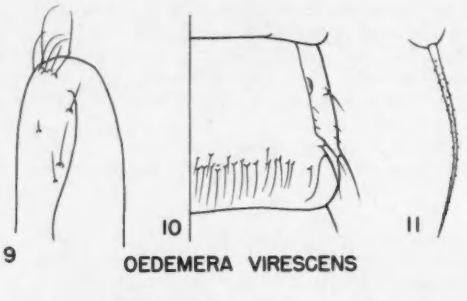


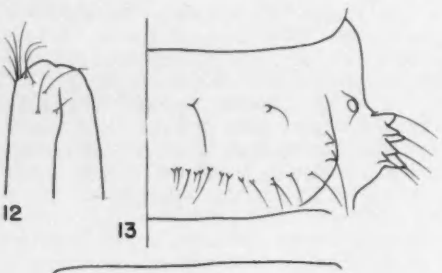


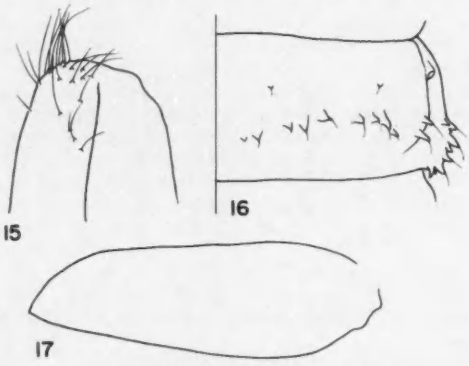










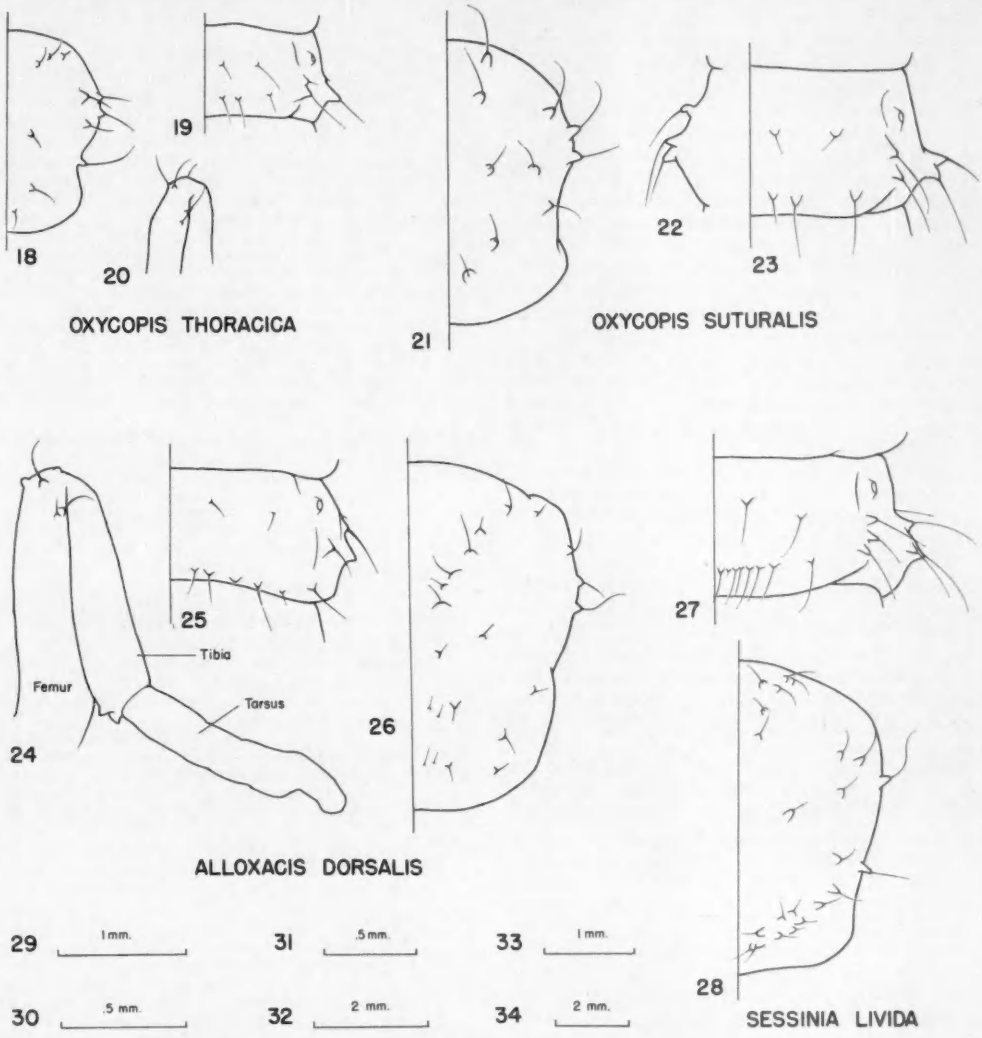


The respective scales for these figures (except Nos. 1, 5, 6, and 11) appear as figures 29–34 on plate 2.

FIG. 1.—Right half of generalized fourth abdominal tergum, dorsal view. FIG. 2.—*Alloxacis dorsalis*, male, posterior tip of abdomen, lateral view. FIG. 3.—Same, ventral view. FIG. 4.—Same, female, ventral view. FIG. 5.—*Pytho americanus*, seta of pronotum. FIG. 6.—*Oxycopis suturalis*, seta of pronotum. FIG. 7.—*Calopus angustus*, knee of anterior left leg, ventral view. FIG. 8.—Same, right half of fourth abdominal segment, dorsal view. FIG. 9.—*Oedemera virescens*, knee of anterior left leg, ventral view. FIG. 10.—Same, right half of fourth abdominal segment, dorsal view. FIG. 11.—Same, plumose seta of fourth abdominal tergum. FIG. 12.—*Nacerdes melanura*, knee of anterior left leg, ventral view. FIG. 13.—Same, right half of fourth abdominal segment, dorsal view. FIG. 14.—Same, left elytron. FIG. 15.—*Ditylus quadricollis*, knee of anterior left leg, ventral view. FIG. 16.—Same, right half of fourth abdominal segment, dorsal view. FIG. 17.—Same, left elytron.

americanus nearly subequal to length of pleural one); meso- and metanotum at most with minute, unpigmented tubercles which are much smaller than largest ones on fourth abdominal tergum (meso- and metanotum in *Othnius umbrosus* and *Melandrya striata* with apically pigmented and sharply pointed tubercles on each side, these tubercles subequal in size to largest tubercle of fourth abdominal tergum); anterior femur (fig. 7) with apical setae not arising from tubercles (these setae in *Eurystethus debilis* arising from large, sharply pointed tubercles).

The characters of the pupae alone are not sufficient to determine to which family or group



The scale for all these figures appears at fig. 29 below.

FIG. 18.—*Oxycopis thoracica*, right half of pronotum, dorsal view. FIG. 19.—Same, right half of fourth abdominal segment, dorsal view. FIG. 20.—Same, knee of anterior left leg, ventral view. FIG. 21.—*Oxycopis suturalis*, right half of pronotum, dorsal view. FIG. 22.—Same, pleural tubercles of left side of fourth abdominal segment, dorsal view. FIG. 23.—Same, right half of fourth abdominal segment, dorsal view. FIG. 24.—*Alloxacis dorsalis*, femur, tibia, and tarsus of anterior leg, ventral view. FIG. 25.—Same, right half of fourth abdominal segment, dorsal view. FIG. 26.—Same, right half of pronotum, dorsal view. FIG. 27.—*Sessinia livida*, right half of fourth abdominal segment, dorsal view. FIG. 28.—Same, right half of pronotum, dorsal view. FIG. 29.—Scale for figs. 2–4, 7, 8, 12, 13, 15, 18–28. FIGS. 30.—Scale for fig. 9. FIG. 31.—Scale for fig. 10. FIG. 32.—Scale for fig. 14. FIG. 33.—Scale for fig. 16. FIG. 34.—Scale for fig. 17.

of families the Oedemeridae are most closely related.

The available pupae of the Oedemeridae, like the larvae, seem to be of three types: (1) *Calopus* (at least some setiferous tubercles sharply pointed and with simple setae arising from subapical position, as in fig. 5); (2) *Ditylus, Nacerdes, Xanthochroa, Oxycopis, Sessinia,* and *Alloxacis* (all setiferous tubercles with setae arising from more or less rounded apices, as in fig. 6, dorsal abdominal setae simple); and (3) *Oedemera* (all setiferous tubercles with setae arising from more or less rounded apices, dorsal abdominal setae microscopically plumose, as in fig. 11). The characters listed for *Calopus* are also possessed by many of the related families, some genera of which are mentioned in the family diagnosis. This fact suggests that *Calopus* may be more closely related to these families than is any other oedemerid. I have mentioned elsewhere (mansucript not yet published) that larval characters also indicate this relationship, and in addition hypothesized that the Calopodinae is the most primitive of the three oedemerid subfamilies. Unfortunately, the pupal characters of *Calopus* as I now understand them do not lend themselves to an evaluation of the primitiveness of the Calopodinae.

Differences in the number, arrangement, and size of the setiferous tubercles have been the most valuable characters for distinguishing the taxa. However, number and position were discovered to be somewhat variable in pupae of *Alloxacis dorsalis* (Melsheimer), the only species represented by a long series of specimens. They must, therefore, be used with caution. In the construction of the key, characters of the tubercles which I thought might be unreliable were omitted. Nevertheless, the key should be considered tentative in view of the few specimens available for study.

Although lack of material has prevented the use of the shape of the terminal abdominal sclerites and urogomphi, these structures may well be of value for distinguishing between species and between genera. It might also be expected that they would be excellent for differentiating families, particularly those whose adults can be separated on the basis of genitalic characters. Since some past describers apparently did not realize that the structures are subject to marked sexual dimorphism, the posterior tips of the abdomen of a male and a female *Alloxacis dorsalis* are illustrated (figs. 2, 3, 4).

The following comments concern characters employed in the key and the illustrations. The apical hairs of the anterior femur were drawn while the pupa rested on its dorsum, with the leg oriented as in figure 24. The generalized pattern of the setiferous tubercles on the dorsum of the fourth abdominal segment is illustrated in figure 1, and the setiferous tubercles are labeled. One or more of the lateral marginal setae occasionally may appear to arise from the membrane immediately laterad of the tergum (which is always weakly sclerotized and often difficult to delimit), rather than from the tergum itself. However, they cannot be confused with the pleural tubercles, since the latter are always situated laterad of the spiracle in dorsal view, or below it in lateral view.

KEY TO KNOWN PUPAE

1. Anterior femur with eight or more apical setae visible in ventral view (figs. 9, 12, 15) 2
   Anterior femur with not more than six apical setae visible in ventral view (figs. 7, 20, 24) .. 4

2 (1). Fourth abdominal tergum (fig. 10) with lateral and posterior margins having approximately 20 setiferous tubercles on each side, their setae (fig. 11) microscopically plumose; discal area of same tergum without setiferous tubercles, though with fine setae; pleural tubercles of all abdominal segments small, inconspicuous (fig. 10) ..... **Oedemera virescens** (Linnaeus)
   Fourth abdominal tergum (figs. 13, 16) with lateral and posterior margins having less than 16 setiferous tubercles on each side, their setae simple; discal area of this tergum with two or more setiferous tubercles on each side; pleural tubercles large and conspicuous on most segments (figs. 13, 16) 3

3 (2). Anterior femur (fig. 15) with approximately 20 apical setae visible in ventral view; each elytron (fig. 17) broad, and gradually narrowing toward apex because of curve of costal margin ..... **Ditylus quadricollis** LeConte
   Anterior femur (fig. 12) with not more than 15 apical setae visible in ventral view; each elytron (fig. 14) narrow, with sides subparallel, and angulate at apex ..... **Nacerdes melanura** (Linnaeus) **Xanthochroa erythrocephala** (Germar)

4 (1). Abdominal pleural tubercles and usually many other body tubercles sharply pointed and with setae arising subapically (as in fig. 5); anterior femur (fig. 7) with apical setae, if present, not arising from tubercles ..... **Calopus angustus** LeConte
   Abdominal pleural tubercles as well as other body tubercles acutely rounded and with setae arising from apex (fig. 6); anterior femur with setae arising from distinct tubercles (figs. 20, 24) 5

5 (4). Pronotum (figs. 18, 21) with approximately 11 setiferous tubercles on each side 6
   Pronotum (figs. 26, 28) with more than 15 setiferous tubercles on each side 7

6 (5). Abdominal segments 3–7 (fig. 19) with a single large pleural setiferous tubercle plus one or more minute ones on each side ..... **Oxycopis thoracica** (Fabricius)
   Abdominal segments 3–7 (figs. 22, 23) with 2 to 4 conspicuous setiferous tubercles on each side ..... **Oxycopis suturalis** (Horn)

7 (5). Fourth abdominal tergum (fig. 27) with lateral and apical margins having total of approximately 11 setiferous tubercles on each side; pronotal tubercles (fig. 28) larger in proportion to size of pronotum ... **Sessinia livida** (Fabricius)
   Fourth abdominal tergum (fig. 25) with lateral and apical margins having total of approximately 7 setiferous tubercles on each side; pronotal tubercles (fig. 26) smaller in proportion to size of pronotum .... **Alloxacis dorsalis** (Melsheimer)

MATERIAL EXAMINED

All of the following pupae are associated with larvae, and many (as indicated) also with adults.

CALOPODINAE

Calopus angustus LeConte: 2 females, Sumpter, Oregon, July 1911, in *Pinus contorta* (F. C. Craighead), Hopk. U. S. 9546. 1 male, Oregon, in yellow pine (F. C. Craighead), Hopk. U. S. 9071e. 1 male, 1 female, Paradise Valley, Mt. Rainier, Washington, 7,000 ft., September 1905, in *Abies lasiocarpa* (H. E. Burke).

NACERDINAE

Nacerdes melanura (Linnaeus): 1 female, Quincy, Massachusetts, 1939 (A. P. Richards), ex timber buried 3–5 ft. below surface of ground for 18 years, No. 39–10578. 2 males, Lancing, Sussex, England (B. G. Rye). 1 male, "Holm's place," Copenhagen, Denmark, June 26, 1924, in old piers (E. Rosenberg).

Xanthochroa erythrocephala (Germar): 1 female, Florida, 1896.

OEDEMERINAE

Ditylus quadricollis LeConte: 1 female, Missoula, Montana, May 13, 1916 (Josef Brunner), Hopk. U. S. 12373 [reared adults in collection of U. S. National Museum].

Alloxacis dorsalis (Melsheimer): 12 males, 12 females, Indian River, Florida, April 22, 1880 [with adults]. 2 females, Florida, in rotten wood, No. 2235 [with adults]. 1 male, 4 females, ocean beach opposite Jupiter Narrows, Florida, 1880, in drift wood. 1 male, Port Isabel, Texas, April 22, 1917, in decaying log of driftwood (T. E. Snyder), Hopk. U. S. 15118b.

Oxycopis thoracica (Fabricius): 1 female, Falls Church, Virginia, Virginia pine, Hopk. U. S. 10080j. 2 males, Damascus, Virginia (T. E. Snyder), Hopk. U. S. 12863.

Oxycopis suturalis (Horn): 1 female, Indian River Inlet, Florida, 1880, from roots of mangrove [adults det. by Arnett, 1956].

Sessinia livida (Fabricius): 1 female, Fatia-po, Meetia Island, Society Islands, May 12, 1934, ex *Hibiscus tiliaceus* (E. C. Zimmerman) [adults det. by E. A. J. Duffy].

Oedemera virescens (Linnaeus): 2 females, Sundby Storskov, Denmark, April 14, 1948, *Eupatorium* (J. P. Kryger) [with adult].

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Böving, A. G., and **F. C. Craighead.** 1931. An Illustrated Synopsis of the Principal Larval Forms of the Order Coleoptera. Brooklyn Ent. Soc., New York. viii+ 351 pp., pls.

Coquerel, Ch. 1848. Observations entomologiques sur divers insectes recueillis à Madagascar. Ann. Soc. Ent. France (2) 6: 177–90, figs. [Pupa of *Sessinia helvola* (Klug) described under *Nacerdes maritima* Coquer.]

Daggy, T. 1947. Notes on the ecology and taxonomy of certain pupae of the family Tenebrionidae (Coleoptera). Proc. Indiana Acad. Sci. 56: 253–60, figs.

Duffy, E. A. J. 1952. The immature stages of *Sessinia livida* (Fabricius). Proc. Hawaiian Ent. Soc. 1951, 14(3): 379–83, figs. [Pupa described.]

Dufour, L. 1841. Histoire des métamorphoses d'une oedémère. Ann. Soc. Ent. France 10: 5–10, fig. [Pupa of *Nacerdes dispar* (Dufour) described under *Oedemera dispar* Dufour.]

Gardner, J. C. M. 1931. Immature stages of Indian Coleoptera (9). Indian Forest Rec. (Ent. Ser.) 16(4): 91–111, pls. [Pupa of *Xanthochroa himalaica* Blair described.]

Heeger, E. 1853. Beiträge zur Naturgeschichte der Insecten. Sitzungsber. kaiserl. Akad. Wiss. 11: 927–42, pls. [Pupa of *Asclera coerulea* (L.) described and illustrated.]

Heqvist, Karl-Johan. 1952. Beiträge zur Kenntnis der Kaferlarven, I. Ent. Tidskr. 73(3–4): 228–30, figs. [Pupa of *Chrysanthia viridissima* (L.) described and illustrated.]

Perris, E. 1863. Histoire des Insectes du Pin Maritime. 532 pages, figs. Soc. Ent. France. [Pupa of *Xanthochora carniolica* (Gistel) described and illustrated, and that of *Nacerdes melanura* (L.) compared with it.]

1877. Larvae de Coléoptères. 590 pages. Paris: Deyrolle. [Pupae of *Oedemera flavipes* (Fabricius), *O. virescens* (L.), and *O. nobilis* (Scopoli) (under *O. coerulea* (L.)) described.]

Schiödte, J. C. 1861–83. De metamorphosi eleutheratorum observationes. Naturhist. Tidskr. vol. 1–13, pls. [Pupae of *Asclera coerulea* (L.) and *Oedemera virescens* (L.) described and illustrated.]

Xambeu, V. 1898. Moeurs et métamorphoses des insectes IX, 1re partie. Revue d'Ent. 17(1–2): 1–63. [Pupa of *Chrysanthia viridissima* (L.) described.]

ERRATUM

On page 113 of Volume 52 (March 1959) the last two sentences of the abstract should read as follows.

Hatching is brought about when the embryo is activated to elevate its hatching spine against the fracture line while applying pressure toward a ventral depression of the cap. Once exposed to the water, the larva rapidly expands and soon swims away.

A SURVEY OF THE EMPOASCA FABAE COMPLEX (HEMIPTERA, CICADELLIDAE)[1]

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ABSTRACT

The internal apodeme of the first sternite and some characters of the second tergite are introduced for discrimination of species in the complex. Phylogenetic trends are discussed and deduced, and a suggested phylogenetic scheme outlined. Distribution of the complex is, with few exceptions, in the American tropics and subtropics; this area was undoubtedly its original home, from which a single species, *Empoasca fabae*, has spread to become strictly a warm-temperate, nontropic species. It is suggested that the diagnostic differences in the apodemes at the base of the male abdomen may be associated with sounds distinctive for each species, which are probably the primary mechanism in maintaining sexual isolation within the complex. A key to the males is followed by descriptions and records of the 21 included species, 13 of which are new to science.

The study of much additional material in the *Empoasca fabae* complex made available since the preliminary report of these insects by Ross and Moore (1957) indicates that less than half of the species in the complex had been discovered at that time. The ensuing studies brought to light not only additional species but several other characters useful in their classification, and the additional species and structures have provided data for a preliminary phylogenetic organization of the complex.

ADDITIONAL DIAGNOSTIC STRUCTURES

In the 1957 paper by Ross and Moore the apodemes of the second sternite and third tergite were used as important diagnostic characteristics. More recent exploration has indicated that in this genus the apodeme of the first sternite also exhibits some remarkably good structural differences. A survey of this apodeme in the *Empoasca fabae* complex and in certain other related complexes, such as that including *sativae*, suggests that the primitive condition of the structure resembles the condition found in *canda*, fig. 1, in which the apodeme is large, has a stout base, an emarginate apical margin, plus fairly narrow apical, lateral, and mesal sclerotized thickenings or bars which give the apodeme a bioculate appearance. In other members of the *fabae* complex numerous deviations from this type can be traced, some involving conspicuous changes in proportions, as in fig. 4, some involving loss of sclerotization, as in fig. 13, and a few involving extreme reduction, fig. 12. There is a marked tendency for this first sternal apodeme to be either much reduced or to lose some of its sclerotization when the second sternal apodemes are small.

According to Ossiannilsson (1949), muscles extend between the first two sternal apodemes. It seems plausible that the different arrangements of unsclerotized areas, diffusely sclerotized areas, and definite bands of heavy sclerotization exhibited in the first sternal apodemes of the various species of the *fabae* complex are associated with differences in the pattern of muscles which are attached to the apodeme. The results of the functional aspects of this structure are discussed later in the paper.

For sake of brevity, the apodemes of the basal abdominal segments are designated throughout the remainder of this paper according to the sclerite from which they arise. Thus the apodeme of the first sternite is called "apodeme 1S," the apodeme of the third tergite is called "apodeme 3T," etc.

Another character found to be of considerable use was the pattern of sclerotization of the second tergite. In most species the mesal portion is fairly simple, fig. 41, but in others this area may be enlarged, fig. 40, or be provided with longitudinal sclerotized thickenings, figs. 38, 39. Differences in these two characters have, in numerous cases, shown that species previously considered to be very close are in reality distantly related.

PHYLOGENETIC TRENDS

As of the present writing 21 species have been diagnosed in the *fabae* complex. Some of these species are obviously extremely close to each other and even a cursory examination shows that a few indubitably monophyletic clusters of species may readily be differentiated. The three species *gibsoni*, *hastosa*, and *cunninghami*, for example, have a peculiar sagittate apex on the brachone combined with other similarities; and *zapoides*, *beckeri*, and *kraemeri* have a distinctive bioculate apodeme 1S combined with an elongate apex of the brachone. This situation encouraged an attempt to arrange the species of the complex into a phylogenetic scheme (chart 1).

Comparing species within the *fabae* complex with species in other complexes, there seems to be no doubt that the primeval ancestor of the complex possessed the following characters:

[1]A contribution from North Central Regional Project NC-29. Accepted for publication October 20, 1958.

apodeme 1S bioculate and emarginate, probably as in *canda*, fig. 1; apodemes 2S extending the length of at least three segments as in *gansella*, fig. 17; apodemes 3T represented by only narrow thickenings as in *gibsoni*, fig. 38, and *tetronis*, fig. 35; and brachone possibly somewhat as in *mergata*, fig. 49. On the basis of characters discovered to date, the morphological similarities and differences found in the *fabae* complex can be explained most reasonably on the assumption that three distinctive lines arose from the ancestor of the complex.

The first line, represented by *canda* and its allies, changed primarily in developing a long and slightly sinuate apical portion of the brachone, figs. 45–46. Except for its slightly shortened apodemes 2S, the species *canda* is remarkably close to what the earliest production of this line could have been and may represent a living fossil having a condition close to this step in the evolution of the group. From a *canda*-like form evolved a series of three species, *zapoides*, *beckeri*, and *kraemeri*, in which apodemes 2S first became parallel-sided (as in *zapoides*, fig. 19), then separated on the meson (as in *beckeri*, fig. 21), and finally became much smaller (as in *kraemeri*, fig. 22). In a side branch of this line stemming from a *canda*-like condition the apical margin of apodeme 1S became straight, heavy, and bar-like, giving rise to the species *gansella*, fig. 5, and *fenestra*, fig. 4; the latter has retained a more massive sclerotization of apodeme 1S but has shorter apodemes 2S, fig. 18.

The species related to *hastosa* and *incoata* seem to form a second major line of the *fabae* complex. All the species in this line have small apodemes 2S, figs. 28–33, and most of the species can be grouped into two clusters of species each showing a regular trend in evolutionary development. In all of these the sclerotization of apodeme 1S is much reduced; at most the lateral bands of the apodeme are quite narrow and the mesal band indicated only faintly, figs. 7, 9. The species *mergata* is similar to the more primitive members of these two clusters in apodemes 2S and somewhat in shape of the brachone; it differs from all of them in the sclerotization of apodeme 1S, having a well-defined narrow mesal band but no trace of the lateral bands, fig. 6. It is probable, therefore, that the *incoata-hastosa* clusters and

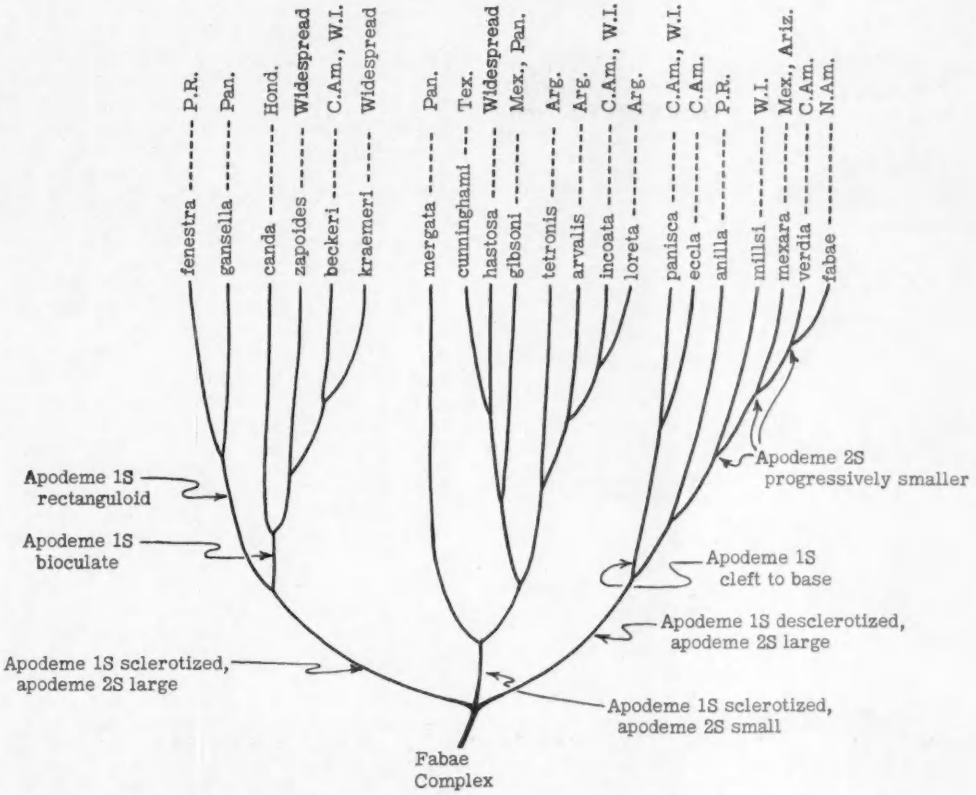
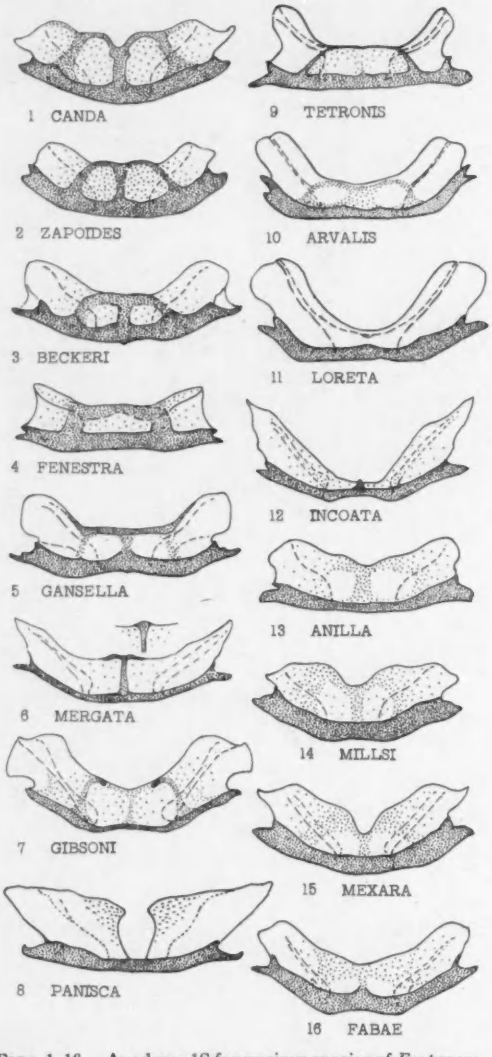
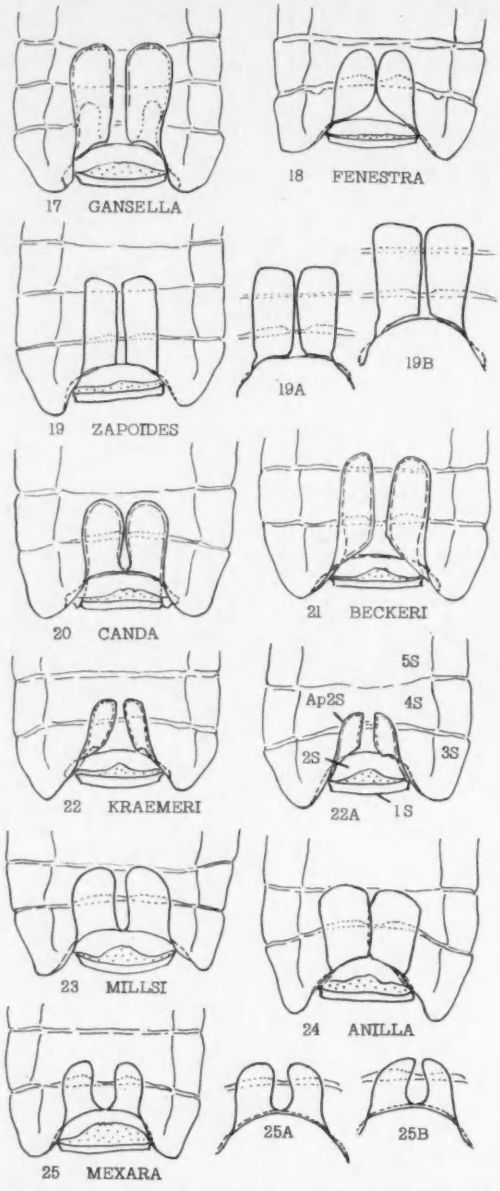


CHART 1.—Suggested phylogenetic outline of the *Empoasca fabae* complex.

mergata arose from a common ancestor in which all three bands of apodeme 1S had become narrowed, and in which apodemes 2S had become greatly shortened. Following the postulate that this was the case, *mergata* would have arisen as a side branch in which the lateral bands of apodeme 1S became lost, and the others would form a branch in which the mesal band became much reduced. The species *tetronis* is very similar to the deduced ancestor of this latter branch. From a *tetronis*-like ancestor arose a more specialized line in which apodemes 2S became successively smaller, first as in *arvalis*, fig. 30, and then to a form in which the apodemes became reduced to mere stubs, as in fig. 31. From such a form there evolved two species, *incoata* in which apodeme 1S became greatly reduced, fig. 12, and *loreta* in which apodemes 3T became considerably enlarged, fig.



FIGS. 1–16.—Apodeme 1S for various species of *Empoasca*.



FIGS. 17–25.—Apodemes 2S for species of *Empoasca*. The outline of the basal abdominal segments has been superimposed around the apodemes, which actually are internal. *A*, *B*: varying conditions of apodemes 2S. *Ap2S*: apodemes 2S. *1S*, *2S*, etc.: first sternite, second sternite, etc.

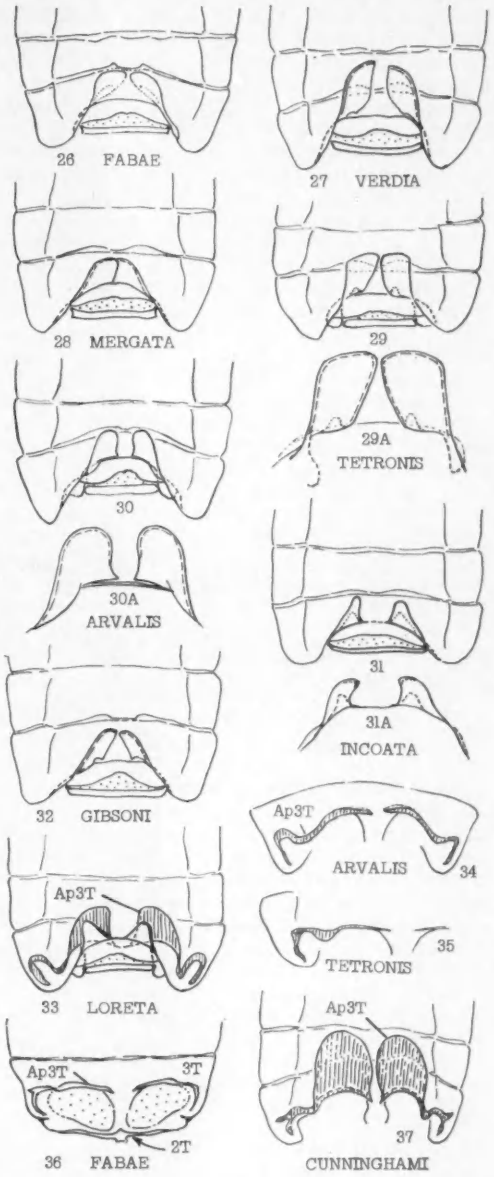
33. Probably also from an ancestor somewhat like *tetronis* and *mergata* arose a branch in which the tip of the brachone became spearlike, as in fig. 50*A*, this branch giving rise first to *gibsoni*, then subsequently to *hastosa* and *cunninghami*, fig. 37, in both of which apodemes 3T became successively larger.

In the third major phyletic line in the *fabae* complex, which culminates in the species *fabae*, the sclerotization of apodeme 1S became extremely diffuse and faint but there was little accompanying decrease in the size of apodeme 1S itself, figs. 13–16, or in apodemes 2S. The long apodemes 2S of the species *anilla*, fig. 24, are suggestive of a fairly early stage in the evolution of this line. Apparently two branches arose from an *anilla*-like ancestor. In the line leading to *fabae* apodemes 2S became successively smaller. The existing steps in this line of change are exemplified by *millsi*, fig. 23, *mexara*, fig. 25, *verdia*, fig. 27, and *fabae*, fig. 26. In the other branch arising from an *anilla*-like ancestor, apodeme 1S became sharply cleft on the meson, fig. 8. Two species represent this branch, *panisca* and *eccla*. *Eccla* is unusual in that it possesses conspicuous apodemes 3T.

A peculiar feature of the evolution of the *fabae* complex is the large amount of parallel evolution which must be invoked to explain the origin and development of the various phyletic lines. If the family tree depicted in chart 1 is even reasonably correct, parallel reductions of apodemes 2S have occurred in all three major lines, and invaginated apodemes 3T have arisen in at least three phyletic lines, exemplified by *eccla* in the *fabae* line, by *loreta* in the *incoata* branch, and by the pair of closely related species *hastosa* and *cunninghami* in the *hastosa* branch. Covergence of this kind may represent spontaneous parallel genetic change occurring independently in each line or it may indicate that in at least some cases the newly evolved characters were transmitted from one line to another by hybridization and introgression. If the latter is involved, the results are expressed as stable mosaic species similar to those reported for the genus *Erythroneura* (Ross 1958). In the *fabae* complex, however, there is not the logical necessity for postulating the hybrid composition of any of the species as there was in the *Erythroneura* cases.

DISTRIBUTION

Reviewing the known records of the species of this complex, it is at once evident that the main distribution pattern embraces primarily the tropics and subtropics of the Americas. Only one species, *fabae*, occurs in and is restricted to the warm temperature region; three other species which extend into this zone, *mexara*, *kraemeri*, and *hastosa*, have their main ranges in warmer zones and extend barely to the southern edge of the warm temperate region. It seems obvious that the *fabae* complex as a whole is of tropical origin and that most of its evolution has taken place in that zone. Several of the species appear to be widespread, but a few have moderately restricted



FIGS. 26–37.—Apodemes at base of abdomen of species of *Empoasca*. FIGS. 26–32, apodemes 2S in relation to base of abdomen, with the enlarged apodemes shown in *A*. FIG. 33, apodemes 2S superimposed over apodemes 3T. FIGS. 34–37, apodemes 3T. *Ap3T*: apodemes 3T. *2T*, *3T*: second and third tergites, respectively.

ranges; remarks in this direction must be considered tentative because of the many tropical areas from which no collections are available. In spite of this deficiency a few circumstances are of interest. The species ***millsi*** is known to date only from the West Indies, its close relative ***mexara*** only from relatively distant Mexico and Arizona; ***verdia*** is known only from Mexico, its close relative ***fabae*** only from north of Mexico; ***cunninghami*** is known only from southern Texas, some distance north of the most northern records of its sister species ***hastosa***; and the two primitive species ***anilla*** and ***fenestra*** are known only from the West Indies. These circumstances suggest that the species in the complex arose originally through the differentiation of populations separated geographically. The trans-Caribbean distribution of five species suggests the probability that isolated populations became established through the dispersal of vagrants rather than because of long-term climatic changes with their accompanying disruptive effects on species ranges. This latter possibility, however, must not be ruled out. Because many species in the complex are extremely closely related it is probable that at least some of them evolved during the Pleistocene, and the geographic isolation producing them may have been brought about by ecological changes accompanying events of the Pleistocene. Before much more can be determined concerning this problem we need to know more about the exact distribution of the ***Empoasca*** species and more about the effect of the Pleistocene on changes in the subtropical belt.

DISTINCTNESS OF SPECIES

The suggested phylogenetic lines described above, the family tree in chart 1 and the illustrations to accompany them emphasize the fact that in the ***Empoasca fabae*** complex, as in many other insect groups, there exist today species differing from each other by remarkably small morphological steps. The question naturally arises: How distinct are these species? Although an exact count is not available, we have studied at least 25,000 cleared specimens of ***Empoasca fabae*** plus about 10,000 specimens of the other species. In this number we have detected no intermediates between the 21 species defined. In several of these species considerable variation occurs but this is either in structures which are not used for diagnostic purposes or is of a sufficiently small range that the conditions existing in one species do not overlap those of another.

The complete distinctness of these species has been impressed upon me repeatedly when sorting light-trap collections made in Puerto Rico by Dr. Irving Fox. These collections contained seven species of the complex including over a thousand males of ***kraemeri***, about 300 of ***zapoides***, 100 of ***millsi***, and small numbers each of ***fenestra***, ***hastosa***, ***anilla***, and ***incoata***. When large numbers of cleared abdomens were arranged side by side in a dish of glycerin the ease with which they fell into these seven species categories was phenomenal.

As a matter of fact, it was this very technique which originally led Dr. Moore and myself to recognize these and other specific segregates in the early phases of our study of the ***fabae*** complex. Large single collections of ***Empoasca*** males were cleared, the abdomens carefully removed and cleaned, then placed in a dish of glycerin. When the abdomens were thus seen side by side in close proximity and in large numbers, both differences and similarities were detected readily.

Similarly large collections from Honduras, Mexico, and Panama exhibited the same mixture of sympatric species with no trace of overlap. It is therefore evident that in the main the species of this complex have widely overlapping ranges and yet remain completely distinct morphologically. Such criteria indicate that the species are not only distinctive but have developed a high degree of genetic isolation.

ISOLATING MECHANISMS

In a group of species so remarkably similar morphologically as those comprising this ***Empoasca fabae*** complex, it seems doubtful if the physiological features of genetic incompatibility would be great enough to prevent the appearance of at least viable if not fertile first-generation hybrids should cross-mating occur. The lack of evidence of such hybrids would seem to be excellent evidence for the existence of rigid barriers to cross-mating, that is, complete sexual isolation. There are other complexes of ***Empoasca***, such as the ***solana*** complex, containing from 10 to 20 closely related species, but in all of these that I have studied the interspecific differences in the male genitalia are of a much greater magnitude than those between most of the species of the ***fabae*** complex. The species of the ***fabae*** complex, on the other hand, exhibit in total a far greater range than those of other complexes in the structures at the base of the abdomen, especially the internal apodemes of the first three segments. This is suggestive of the possible mechanism of sexual isolation in this complex.

In his most illuminating studies on the sound production of Homoptera, Ossiannilsson (1949) has demonstrated that species of ***Empoasca*** produce distinctive sounds and that these are controlled by the muscles attached to the apodemes arising from the basal segments of the abdomen. Presumably species with different lengths and shapes of apodemes have correspondingly different musculature and produce different sounds. Ossiannilsson does record distinctive sets of sounds produced by the three species of ***Empoasca*** upon which he reported. Fulton (1952), Alexander (1957), and Alexander and Moore (1958) have

shown that in certain crickets and cicadas the mating calls of closely related species are far more distinctive than are the slight morphological differences between them. These results, plus the apodemal differences in the species of the *fabae* complex, suggest strongly that the species of this latter group also have distinctive mating calls and that this is an important mechanism by which sexual isolation is maintained. In frogs in the genus *Microhyla*, Blair (1955) demonstrated that range overlap was a potent factor in reinforcing mating-call differences between different species.

It is therefore possible to theorize that by a series of geographic isolations the original ancestor of the *fabae* complex evolved into a progressively larger number of species which were very similar morphologically but incompatible genetically. Because under these conditions a breakdown in sexual isolation leading to hybridization would lead to gametic wastage, selection pressures presumably occurred which tended to increase any traits which would insure or reinforce sexual isolation whenever the ranges of these species came into contact or overlapped. It seems reasonable to assume that in this *fabae* complex these reinforcing factors, as Sibley (1957) calls them, took the form of distinctive mating calls and these in turn were brought about by changes in the shape and musculature of the basal abdominal apodemes associated with the sound-producing mechanism.

KEY TO SPECIES

1. Dorsal apodemes large and crescentic or lobate, figs. 33, 37 2
   Dorsal apodemes linear, figs. 34–36, 42, 43 5
2. Apex of brachones elongate and either straight and narrow, fig. 51, or pointed and spear-shaped, fig. 50 3
   Apex of brachones short, occasionally narrow but never spear-shaped 4
3. Apodemes 3T crescentic, not extending into next segment (Ross & Moore 1957, fig. 1) ..... **hastosa**
   Apodemes 3T saclike, extending well into next segment, fig. 37 ..... **cunninghami**
4. Apodeme 1S sharply cleft to its base on meson, fig. 8; apodemes 2S extending into fourth segment **eccla**
   Apodeme 1S evenly emarginate, fig. 11; apodemes 2S not extending to fourth segment, fig. 33 .. **loreta**
5. Sternal apodemes not extending beyond third segment 6
   Sternal apodemes longer, extending into fourth segment 10
6. Second tergite with sclerotized longitudinal bars, fig. 38; apex of brachone spear-shaped, fig. 50; apodeme 1S as in fig. 7 ..... **gibsoni**
   Second tergite with sclerotized bars diagonal or inconspicuous, figs. 40, 41; apex of brachone blunt; apodeme 1S otherwise 7
7. Apodemes 2S far apart and tubercle-like, fig. 31; apodeme 1S with mesal area dished in almost to base, fig. 12 ..... **incoata**
   Apodemes 2S closer together and flaplike, figs. 26, 28; apodeme 1S reduced no more than in fig. 10 8
8. Apodeme 1S with mesal bar sclerotized, lateral bars indistinct, fig. 6 ..... **mergata**
   Apodeme 1S with mesal bar, and sometimes lateral bars also, indistinct, figs. 10, 16 9
9. Apodemes 2S ovate, widened slightly toward base, and well separated at apex, fig. 30; apodeme 1S with lateral bands and apical margin narrowly but distinctly sclerotized, fig. 10 ..... **arvalis**
   Apodemes 2S clavate, narrowed at base but nearly touching at apex, fig. 26; apodeme 1S with only indistinct sclerotization, fig. 16 ..... **fabae**
10. Apodeme 1S with a sharp median cleft to its base, fig. 8; apex of brachone only one-third length of brachone (Ross & Moore 1957, fig. 16*A-C*) .. **panisca**
    Apodeme 1S with apical emargination no deeper than in figs 4, 5, 15 11
11. Apodeme 1S with apical margin and sometimes the median and lateral bars also heavily sclerotized, figs. 1–4 12
    Apodeme 1S with apical margin only slightly, fig. 9, or not at all sclerotized, figs. 13–16 17
12. Apodeme 1S with sclerotized areas forming a low rectangle, sometimes with the lateral or mesal bars indistinct, figs. 4, 5 13
    Apodeme 1S with sclerotized areas forming a bioculate shape, all bars well sclerotized, figs. 1–3 .. 14
13. Apodemes 2S extending to apex of segment 5, only slightly narrowed toward base, fig. 17 .... **gansella**
    Apodemes 2S extending only through segment 4 and constricted at base, fig. 18 ..... **fenestra**
14. Apodemes 2S small, distant at base, and extending at most midway into fourth segment, fig. 22 .... **kraemeri**
    Apodemes 2S much larger, either extending into fifth segment, fig. 21, or approximate at base, fig. 20 15
15. Apodemes 2S ovate and not reaching fifth segment, fig. 20; apodeme 1S with a marked but narrow mesal notch on apical margin, fig. 1 ..... **canda**
    Apodemes 2S parallel-sided or straight-sided, extending slightly into fifth segment, figs. 19, 21; apodeme 1S with only inconspicuous apical emargination, figs. 2, 3 16
16. Apodemes 2S nearly truncate at apex and not narrowed sharply near base, fig. 19 ..... **zapoides**
    Apodemes 2S rounded or markedly oblique at apex, and narrowed sharply near base, fig. 21 .... **beckeri**
17. Apodemes 2S wide, extending almost or fully to apex of fifth segment, figs. 23, 24 18
    Apodemes 2S extending only a short distance into fifth segment, sometimes narrow, figs. 25, 27, 29 .. 19
18. Apodemes 2S straight-sided and contiguous, fig. 24 **anilla**
    Apodemes 2S rounded, their mesal margins concave and not contiguous on meson except at base and occasionally at apex, fig. 23 ..... **millsi**
19. Apodemes 2S wide and almost touching at extreme base, fig. 25 ..... **mexara**
    Apodemes 2S narrowed at base, the bases distant, figs. 27, 29 20
20. Apodemes 2S approaching trapezoidal in shape, fig. 29; apodeme 1S with faint indications of narrow sclerotized lateral bars, fig. 9 ..... **tetronis**
    Apodemes 2S roughly elliptic in shape, fig. 27; apodeme 1S with only diffuse sclerotization, as in fig. 15 ..... **verdia**

DESCRIPTIONS AND RECORDS

This section contains descriptions of the new species encountered in the *fabae* complex since the studies reported by Ross and Moore (1957). In addition new records are listed and illustrations and descriptions of some additional characters are given for the eight species of the complex reported in that paper.

Except where noted, types designated in this paper are in the Illinois Natural History Survey.

Where available, representative paratypes will be deposited in the U. S. National Museum and in the D. M. DeLong collection.

Empoasca canda Ross and Moore

This species was described originally from a scattering of males from several localities. Further study of large series, especially those collected in Puerto Rico by Irving Fox, has demonstrated that two species were confused in the original series of *canda*. One species is represented only by the holotype, from 12 km. west of Olanchito, Honduras. The entire series of paratypes belongs to the species described here as *zapoides*. Distinctive features of *canda* include apodeme 1S, fig. 1, which has well-developed central and lateral sclerotized bands, and the ovate, contiguous apodemes 2S, fig. 20, which extend nearly to the apex of the fourth segment.

Empoasca zapoides, new species

Male.—Size, color, and general structure typical for the *fabae* complex as follows: length 3.5 mm.; color in life pale green with inconspicuous translucent markings on the head and thorax; male genitalia with simple aedeagus, with hook of tenth segment enlarged at base and produced into a narrow ventral point, and style oblique at tip and bearing only a few short lateral setae. Base of abdomen with second tergite and apodemes 3T much as in *fabae*, fig. 36, without unusual specializations. Apodeme 1S, fig. 2, well developed, with definite sclerotized lateral and mesal thickenings which fuse along the apical margin to form a bioculate appearance. Apodemes 2S, fig. 19, extending into fifth segment and close together or slightly separated; the sides of each apodeme are comparatively straight and the apex is also somewhat straight, giving the apodemes a rectangular appearance unusual for the group; some variation occurs in general shape as illustrated in figs. 19*A* and 19*B*, but even in forms such as that illustrated in fig. 19*B*, in which the apodemes are wider at the apex, the straight sidedness is still evident. Brachone, fig. 45, elongate and slender, the extreme tip occasionally slightly more sinuate.

Holotype male.—Isla Verde near San Juan, Puerto Rico, July, 1957, at light, Irving Fox. *Paratypes.*—COLOMBIA: Medellin, Ant., November 7, 1956, on beans, R. F. Ruppel, 1 ♂. CUBA: Santiago de Las Vegas, October 1956, on beans, Valdez Barry, 1 ♂. HONDURAS: 12 km. west of Olanchito, July 7-September 7, 1949, at light, E. C. Becker, 5 ♂. PANAMA: Ft. Gulick, December 14, 1956, at light, W. H. Wymer, 2 ♂; same but January 14-February 8, 1957, R. M. Altman, 4 ♂; Ft. Cobbe, January 3–7, 1957, at light, R. M. Altman, 4 ♂; Headquarters 15th N. D., November 30, 1956, at light, W. H. Wymer, 2 ♂; Canal Zone, June 20–24, 1957, at light, R. M. Altman, 1 ♂. PUERTO RICO: Same data as for holotype but October 1956, and at monthly intervals from September 1957 to July, 1958, 234 ♂.

This species is most closely related to *canda* and *beckeri*. In *canda* apodemes 2S extend only into the fourth sternite and are rounded, whereas in *zapoides* apodemes 2S are longer and somewhat straight sided; furthermore in *canda* apodeme 1S has a deep mesal notch on its apical margin whereas in *zapoides* apodeme 1S has only a slight excavation on the apical margin. In *beckeri* sternites 2S, although somewhat straight sided for most of their length, have a narrowed apex and are conspicuously narrowed near the base.

E. zapoides appears to be widespread through the West Indies and Central America. Judging from the light trap catches made by Dr. Fox, it is one of the common components of the *Empoasca* fauna in the vicinity of San Juan, Puerto Rico, and frequently is second in numerical abundance of all the species of *Empoasca* taken in that area. Our only records associated with the host, *Phaseolus* beans, consist of single specimens each, giving little clue as to the host relationships of this species.

Empoasca beckeri, new species

Male.—Similar in size, color, and general structure to the preceding species. Base of abdomen with simple tergites, apodeme 3T represented by only narrow sclerotized thickenings. Sternite 1S, fig. 3, very much as in *zapoides*, but in the holotype of *beckeri*, fig. 3, the mesal and lateral sclerotized thickenings are slightly wider than those in the holotype of *zapoides*, fig. 2. Apodemes 2S, fig. 21, extending slightly into the fifth segment, the sides of each apodeme somewhat straight and nearly parallel-sided but with the tip of each rounded and the base narrowed. Hook of tenth segment with tip set off a little more abruptly from the base than the condition illustrated in fig. 44. Brachone, fig. 46, long and narrow, the apical portion nearly as long as the basal portion and its narrowed upper part slightly sinuate and curved laterad at the tip.

Holotype male.—Camp Pina, Republic of Panama, June 7, 1955, at light, R. M. Altman. *Paratypes.*—PANAMA: Same data as holotype, but May 23-June 7, 1955, 3 ♂, Ft. Gulick, February 22, 1957, 2 ♂. PUERTO RICO: Isla Verde near San Juan, June-July 1958, at light, Irving Fox, 3 ♂.

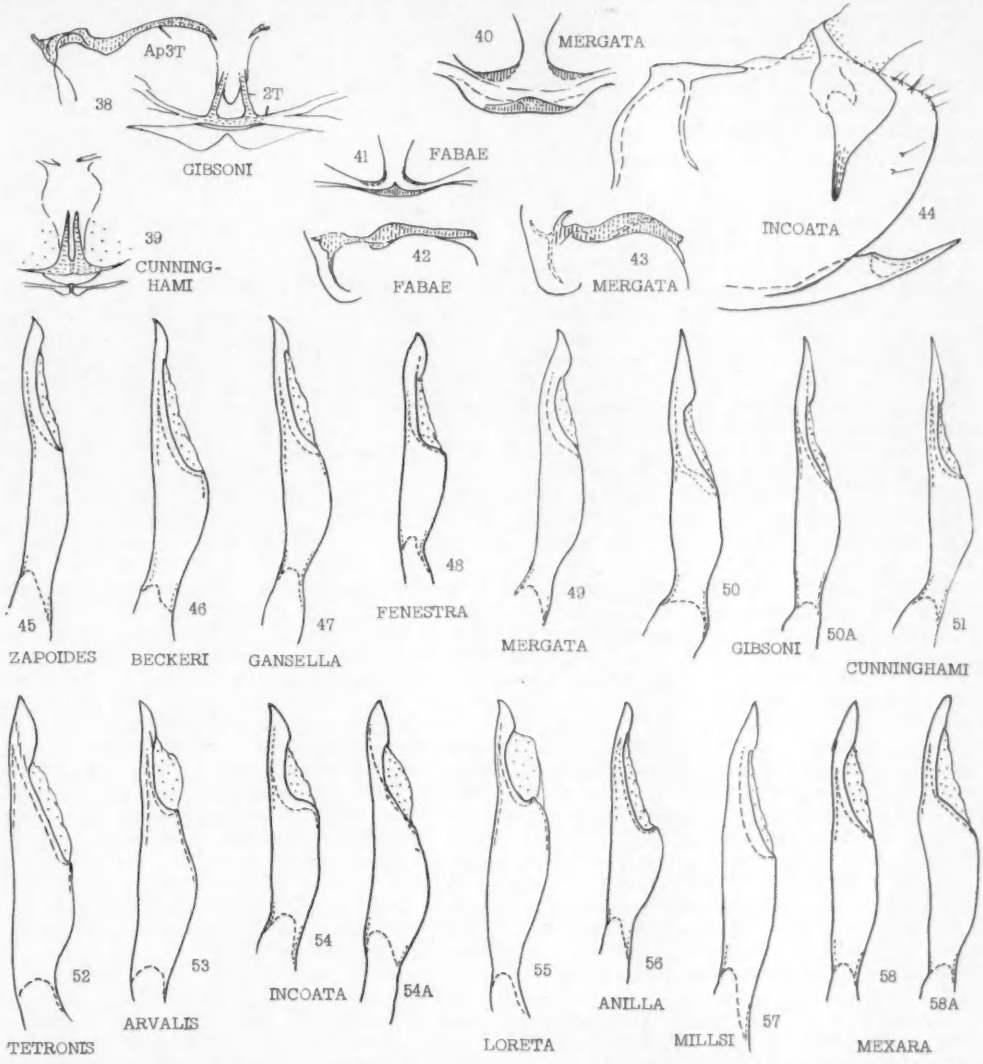
The bioculate apodeme 1S indicates that this species belongs in the series associated with *zapoides*, from which *beckeri* differs primarily in the shape of apodemes 2S which are narrowed at the base and are held a little farther apart than in *zapoides*. In other features of the genitalia, *beckeri* is also similar to *kraemeri* from which it differs in the much larger apodemes 2S. Apodemes 2S in *kraemeri* resemble in general proportions and appearance those of *beckeri*, which latter

would therefore appear to be a forerunner of *kraemeri*.

Empoasca kraemeri Ross and Moore

Since the original description of this species (Ross and Moore 1957) a large amount of new material has been studied. Apodeme 1S is almost identical with those of *zapoides* and *beckeri* (see figs. 2, 3). The small apodemes 2S are remarkably constant within the limits indicated by figs. 22 and 22*A*. Fig. 22 is of a specimen from Panama and illustrates a slightly longer pair of apodemes, a condition fairly typical of continental populations; fig. 22*A* illustrates a specimen from San Juan, Puerto Rico, and is typical of the slightly shorter apodemes which predominate in the large Puerto Rican samples. As mentioned in the previous description, these apodemes in *kraemeri* appear to be a diminutive form of those in *beckeri*, but in the thousand or more specimens of *kraemeri* studied no indication of intermediates has been encountered.

At the time of the original description, records of this species were listed from Colombia to



FIGS. 38–58.—Sternal apodemes and parts of the male genitalia of species of *Empoasca*. FIGS. 38–41, details of second tergite. FIG. 42, 43, right apodeme 3T. FIG. 44, lateral view of pygofer and left hook of tenth segment. FIGS. 45–58, posteroventral aspect of left brachone. *A*: variants.

Florida. Additional material sent to us from the U. S. National Museum contains records for additional South American countries as follows: Argentina (Loreto, Misiones), Ecuador (Pomasqui), and Peru (Lima). This constitutes the largest range of any known species in the *fabae* complex. In addition *kraemeri* is certainly the most abundant species of the complex in some localities.

Empoasca gansella, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with simple first tergite and only a linear apodeme 3T. Apodeme 1S, fig. 5, with a stout basal bar, with poorly defined lateral and mesal sclerotized bands, but with a long and nearly straight bar comprising the central part of the apical margin; the effect of this pattern is to produce a somewhat rectangular middle piece constituting the central part of the apodeme. Apodemes 2S extending through segment 5 and touching the sutures separating segments 5 and 6, fig. 17; each apodeme is narrowed at the base and rounded at the apex; the two apodemes are well separated on the meson and their mesal margins are straight almost to their base. Brachone, fig. 47, long and slender, the apical narrowed portion as long as the basal portion, and sinuate, curved slightly laterad at tip.

Holotype male.—Ft. Gulick, Canal Zone, Panama, January 14, 1957, at light, R. M. Altman. *Paratypes.*—PANAMA: Camp Pina, June 7, 1955, at light, R. M. Altman, 1 ♂; Ft. Gulick, December 1, 1956-February 22, 1957, at light, R. M. Altman, 3 ♂.

The somewhat rectangular central body of apodeme 1S separates this species from all of the members of the complex with the exception of *fenestra*, from which *gansella* differs in the very much longer apodemes 2S. The long apodemes 2S indicate that this is one of the most primitive members of the complex, and the long sinuate apical region of the brachone indicates a close relationship with *canda* and its allies. The specialized rectangular nature of apodeme 1S in conjunction with its primitive characters would therefore indicate that *gansella* was the base of a side branch representing an offshoot from an early part of the family tree.

Empoasca fenestra, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with simple second tergite and linear apodeme 3T. Apodeme 1S, fig. 4, with a stout basal bar and with a central rectangular area conspicuously delineated by stout sclerotized thickenings consisting of short lateral bars and a long central portion of the apical margin; the mesal sclerotized band is either absent or very faintly indicated. Apodemes 2S, fig. 18, extending nearly to the apex of the fourth segment, contiguous on the meson, each apodeme ovate but narrowed toward the base, having an over-all elongate, droplike shape. Hook of tenth segment with narrowed apical portion set off from the larger base more sharply than illustrated in fig. 44. Brachone, fig. 48, with narrowed apical portion as long as basal portion, the tip fairly heavy and curved mesad more than laterad, with only the faintest suggestion of a sinuate outline.

Holotype male.—Isla Verde near San Juan, Puerto Rico, October-November 1957, at light, Irving Fox. *Paratypes.*—PUERTO RICO: Same data as holotype but May-June 1958, 1 ♂, and June-July 1958, 1 ♂.

The combination of rectangular and heavily sclerotized central rectangle on apodeme 1S and ovate apodemes 2S set this species off from all others in the genus. Apodeme 1S suggests a relationship with *gansella* although the brachone is not so slender or sinuate as in that species. In chart 1 the species has been placed tentatively according to the relationship suggested by apodeme 1S.

Empoasca mergata, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with second tergite, fig. 40, deeper and more massive than in *fabae*, fig. 41; in *mergata* the anterior margin of the tergite is bowed out considerably and the posterior margin at the base of the central strap has an arcuate thickening on each side of the strap. Apodeme 3T, fig. 43, not invaginated but much thicker than the slender type found in *fabae*, fig. 42. Apodeme 1S, fig. 6, with only a moderately thin basal bar, with a thin mesal sclerotized strap, no lateral straps evident and only occasionally with a slight extension of the sclerotization of the apical margin on either side of the mesal bar. Apodemes 2S, fig. 28, short, not extending beyond segment 3, each apodeme somewhat quadrate in general outline, the two approximate on the meson. Hook of tenth segment with apical portion set off more sharply from the basal portion than shown in fig. 44. Brachone, fig. 49, with narrowed apical portion shorter than basal portion, curved chiefly mesad but with the extreme tip curved slightly laterad, giving the apical portion a slightly sinuate appearance.

Holotype male.—Ft. Gulick, Canal Zone, Panama, February 8, 1957, at light, R. M. Altman. *Paratypes.*—PANAMA: Same data as for holotype but February 22, 3 ♂.

The curious apodeme 1S, fig. 6, with its lone central sclerotized bar sets off this species immediately from all others. The whole apodeme is drawn from the holotype; a slight variant condition of the apex of the mesal bar is illustrated in the inset. The short apodemes 2S suggest a relationship with the *tetronis* and *gibsoni* branches,

as outlined in the preceding discussion of the phylogeny.

Empoasca tetronis, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with second tergite simple and not enlarged, and apodemes 3T, fig. 35, unusually slender. Sternite 1S, fig. 9, with stout basal bar but with other sclerotization relatively weak except for the basal portion of the lateral bars; the central portion of the apical margin is sufficiently well sclerotized that this region and the lateral bars mark off a central area quite definitely even though with narrow boundaries; the mesal bar is usually indicated only as a slight darkening. Apodemes 2S, fig. 29, 29*A*, extending slightly into segment 4, the two nearly touching at the apex but well separated at the base; each apodeme, fig. 29*A*, is somewhat trapezoidal in shape because the sides are only slightly curved. Hook of tenth segment very similar to that in fig. 44. Brachone, fig. 52, with apical narrowed portion almost as long as basal portion, unusually stout and fairly straight.

Holotype male.—Loreto, Misiones, Argentina, December 1, 1931, A. A. Ogoblin. *Paratypes.*—Same data as for holotype but November 29-December 6, 6 ♂. Holotype and a series of paratypes in the collection of the Lillo Institute, Tucumán, Argentina, other paratypes deposited in the U. S. National Museum and the Illinois Natural History Survey.

This species is very similar in many ways to *mergata* but differs in the longer apodemes 2S and the quite different pattern of sclerotization in apodeme 1S.

Empoasca arvalis, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with simple second tergite but with apodemes 3T, fig. 34, considerably thicker and more arcuate than in *tetronis*. Apodeme 1S, fig. 10, in general outline very similar to that of *tetronis* but with the pattern of sclerotization indicated only as colored areas; the mesal band is wide and very diffuse. Apodemes 2S, fig. 30, extending only across segment 3, and separated by a wide distance on the meson; each apodeme, fig. 30*A*, is ovate and rounded at the apex but the mesal margin is sclerotized equally with the lateral margin. Hook of tenth segment very similar to that in fig. 44. Brachone, fig. 53, with apical portion only half length of basal portion, the apex fairly straight.

Holotype male.—Loreto, Misiones, Argentina, December 1, 1931, A. A. Ogoblin. *Paratypes.*—Same data as for holotype but November 25-December 18, 25 ♂. Holotype and a series of paratypes in the collection of the Lillo Institute, Tucumán, Argentina, other paratypes deposited in the U. S. National Museum and the Illinois Natural History Survey.

Empoasca loreta, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with second tergite simple, much as in *fabae*. Apodemes 3T, fig. 33, invaginated to form a pair of wide rounded lobes, well separated on the meson, usually extending slightly into segment 4 but occasionally extending scarcely beyond the apex of segment 3. Apodeme 1S, fig. 11, with practically no sign of sclerotization representing the lateral and mesal arms, the apical margin forming an evenly arcuate excavation which comes close to the basal bar at the center of the apodeme. Apodemes 2S, fig. 33, short, triangular, and widely separated on the meson, not extending beyond the apex of segment 3. Hook of tenth segment similar to that illustrated in fig. 44. Brachone, fig. 55, with apical portion only half length of basal portion, the narrowed apical part slightly sinuate and thickened at the tip; the mesal membrane at the apex is unusual in this species in having a thin mesal strip which is slightly sclerotized, especially at the base, a feature which is usually seen readily at fairly low magnifications.

Holotype male.—Loreto, Misiones, Argentina, December 3, 1931, A. A. Ogoblin. *Paratypes.*—Same data as for holotype but November 27-December 18, 39 ♂. Holotype and a series of paratypes in the collection of the Lillo Institute, Tucumán, Argentina, other paratypes deposited in the U. S. National Museum and the Illinois Natural History Survey.

Empoasca incoata, new species

Male.—Length 5 mm. Color and general structure typical for the *fabae* complex. Base of abdomen with second tergite simple, much as in *fabae*, apodemes 3T poorly developed and linear. Apodeme 1S, fig. 12, greatly reduced, with no apparent sclerotization except for the basal bar, the central portion excavated so that only a narrow strip of membrane extends across the middle of the segment. Apodemes 2S, fig. 31, almost vestigial, far apart on the meson and extending at most across segment 3; in the holotype, fig. 31*A*, each apodeme is rounded and curved slightly mesad, but in many other specimens the two apodemes are irregular stubs, the two often dissimilar, fig. 31. Hook of tenth segment with a large base tapering fairly gradually into the narrowed apical portion, fig. 44. Apodeme fairly heavy and wide, usually having the apical portion forming a definite step with the basal portion, fig. 54, in which case the apical portion is considerably shorter than the basal portion. In other specimens the apex merges more gradually into the base, fig. 54*A*, in which case the apical portion appears proportionately longer.

Holotype male.—Canal Zone, Panama, June 20–24, 1957, at light, R. M. Altman. *Paratypes.*—PANAMA: Same data as for holotype, 3 ♂; Navy

Ordinance Depot, August 2, 1955, at light, R. M. Altman, 1 ♂. PUERTO RICO: Isla Verde near San Juan, May-June 1958, at light, Irving Fox, 2 ♂; same but June-July 1958, 22 ♂.

Similarities of apodeme 1S plus the common characters of short apodemes 2S and fairly broad brachone, indicates without much doubt that *incoata* is one of the end products of a South American evolutionary branch starting from an ancestral form somewhat like *tetronis*. From these allies, *incoata* differs from *tetronis* and *arvalis* in its reduced apodeme 1S and from its nearest relative *loreta* in lacking the invaginated apodemes 3T which are such a distinctive feature of *loreta*. *Incoata* is readily identified among all members of the *fabae* complex by its larger size, which varies from 5–6 mm. in contrast to a maximum of little more than 4 mm. found in other species of the complex. Although this difference does not appear great numerically, it shows up with remarkable clarity in a mixed collection of specimens.

The resemblance between figs. 54 and 54*A* and the drawings of the brachone given by Caldwell (Caldwell and Martorell 1952) for *fabae* suggests strongly that this was the species which Caldwell illustrated in his report on the group for Puerto Rico.

Empoasca gibsoni, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with second tergite, fig. 38, having a large anterior pair of pale flaps and having a pair of lateral sclerotized thickenings extending on each side of the mesal flap, these thickenings joined at the base by a similar thickening extending across the mesal part of the second segment. Apodemes 3T, fig. 38, not invaginated but forming a fairly thick sinuate thickening. Apodeme 1S, fig. 7, with fairly slender basal bar and faint sclerotized bars across the main body of the apodeme; the lateral bars are always slightly darker than the apical and mesal bars, all of them faint except for one spot on each side where the lateral bar seems to curve mesad and form a small, heavily pigmented area as indicated in the illustration. Apodemes 2S, fig. 32, short, not extending beyond segment 3, widely separated at the base but in cleared specimens often almost meeting at the apex; each apodeme is nearly twice as long as wide, almost parallel-sided, with the apical lateral corner rounded and the apical mesal corner fairly sharp and with only the lateral margin fairly heavily sclerotized. Hook of tenth segment with apical portion longer and set off from the base more abruptly than illustrated in fig. 44. Brachone, fig. 50, with apical portion about equal in length to basal portion, the tip enlarged, pointed, and spear shaped, varying between the more massive extreme illustrated in fig. 50 and the narrower type illustrated in fig. 50*A*.

Holotype male.—Cotaxtla, Veracruz, Mexico, September 10, 1957, from *Canavalia* (Mocuna), W. W. Gibson. *Paratypes.*—MEXICO: Same data as for holotype, 6 ♂; same data but *Mimosa* species, 4 ♂; same data but *Acacia* species, 3 ♂; same data but *Crotalaria* species, 1 ♂. PANAMA: Madden Dam, Canal Zone, June 15, 1946, A. O. Meyer, 1 ♂.

This species is a close relative of *hastosa*, differing from it in the undeveloped apodemes 3T, the larger and more regular apodemes 2S and the wider sagittate apex of the brachone. The three species *gibsoni*, *hastosa*, and *cunninghami* form a closely-knit branch illustrated in the progressive development of apodemes 3T.

Empoasca hastosa Ross and Moore

Since the original description of this species, numerous additional specimens have been identified but these add records of only one additional country to the known range. Numerous scattered specimens have been taken at Isla Verde near San Juan, Puerto Rico, in the light trap material collected by Dr. Fox. The total known range is now Honduras, Mexico, Panama, Puerto Rico, and U. S. A. (Florida).

It is interesting that in this species apodeme 1S is reduced almost as much as in *incoata* (see fig. 12), a development possibly correlated with the extreme reduction and vestigiality of apodemes 2S in both species.

Empoasca cunninghami, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with the second tergite highly specialized, fig. 39; the sclerotized thickenings along the edge of the mesal strap are close together and appear to form a central sclerotized portion of the tergite from which extend two posteriorly directed sclerotized points. Apodemes 3T, fig. 37, invaginated to form a pair of long ovate flaps, close together on the meson and extending almost to the apex of segment 4. Apodeme 1S greatly reduced, much as in *incoata* (see fig. 12). Apodemes 2S reduced to small vestiges which are similar to those previously illustrated for *hastosa* (Ross and Moore 1957, fig. 7). Hook of tenth segment with basal portion sharply constricted as in *hastosa* (see Ross and Moore 1957, fig. 15*D*). Brachone, fig. 51, with apical portion about the same length as basal portion, the tip elongate, sharp, and narrowly sagittate.

Holotype male.—Pharr, Texas, October 15, 1957, on morning glory, Decker and Mills.

In almost all respects this species is similar to *hastosa* but differs from it in two quite remarkable characters: in *cunninghami* the second tergite has the approximate and conspicuous sclerotized thickenings as in fig. 39, whereas in *hastosa* these thickenings are much less conspicuous and well separated as in *gibsoni* (see fig. 38); and in

cunninghami apodemes 3T are greatly expanded areas, whereas in *hastosa* they form small crescents which do not extend quite to the apex of segment 3 (Ross and Moore 1957, fig. 1).

Empoasca anilla, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with first tergite simple and apodemes 3T represented by only slender sclerotized thickenings. Apodeme 1S, fig. 13, with well-developed basal bar, the remainder of the apodeme large in extent but almost completely membranous; the mesal and lateral bars are indicated only by faint and diffuse darkened areas. Apodemes 2S, fig. 24, extending to the apex of the fourth segment, and touching the meson; each apodeme is wide, nearly straight sided, and rounded at the apex. Hook of tenth segment very similar to that in fig. 44. Brachone, fig. 56, with apical portion nearly as long as basal portion, curved mesad at apex.

Holotype male.—Isla Verde near San Juan, Puerto Rico, October-November 1957, at light, Irving Fox. *Paratype.*—Same data but May-June, 1 ♂.

The large but desclerotized apodeme 1S groups this species with the *millsi-fabae* series. From all these *anilla* differs in the approximate and wider apodemes 2S.

Empoasca millsi, new species

Male.—Size, color, and general structure typical for the *fabae* complex. Base of abdomen with second tergite simple and apodemes 3T represented by only slender sclerotized lines. Apodeme 1S, fig. 14, with massive base and large expanse, but membranous except for faint colored indications of the mesal and lateral bars; the apical margin is broadly emarginate on the meson. Apodemes 2S, fig. 23, extending to apex of segment 4, nearly touching at base but fairly well separated on the meson at other points; each apodeme has rounded sides and apex but a concave mesal margin, and thus is slightly constricted just beyond the base and slightly widened at the extreme base. Hook of tenth segment much as in fig. 44. Brachone, fig. 57, with apical portion about equal in length to basal portion, the tip curved slightly mesad.

Holotype male.—Port-au-Prince, Haiti, May 22, 1950, at light, H. B. Mills. *Paratypes.*—HAITI: Same data as holotype but May 23, 1 ♂. PUERTO RICO: Isla Verde near San Juan, July 1957-July 1958, Irving Fox, 103 ♂.

On the basis of similarities in sternite 1, the brachones, and the general shape of sternite 2, *millsi* is most closely related to *mexara*, differing from it, however, in the larger apodemes 2S which are not only more massive but have more heavily sclerotized lateral and mesal margins. Although this difference might seem to be small, the two specimens from Haiti and the large series from Puerto Rico vary only slightly in this regard and do not approach the condition found in the mainland species *mexara*.

Empoasca mexara Ross and Moore

Apodeme 1S of this species, fig. 15, is extremely similar to that of *millsi* and like it has a deep mesal invagination of the apical margin. Apodemes 2S, fig. 25, appear to be a diminutive condition of that found in *millsi*. Examination of additional series from Arizona and Mexico indicates a range of variation in the shape of these apodemes as indicated in figs. 25, 25*A*, and 25*B*, the latter two specimens from the same series collected at Chapingo, Mexico. Although there is some variation in the shape of the apodemes, specimens we have seen show no tendency for them to become longer and massive as they are in *millsi*. Furthermore, the mesal margins of the apodemes of *mexara* are almost always poorly sclerotized (but not membranous) so that they can be seen sharply usually only with the aid of a compound microscope.

To date this species has been collected only in Mexico and Arizona, where it is sometimes abundant on alfalfa.

Empoasca verdia Ross and Moore

No additional specimens of this species have been encountered since the time of its original description from Honduras and Mexico. Sternite 1S is almost exactly like that of *mexara* (see fig. 15) as are also the second and third tergites. This places *verdia* definitely in the *anilla-fabae* series in which it is diagnosed by the shape of apodemes 2S, fig. 27, with their membranous mesal margins.

Empoasca fabae (Harris)

This common North American form has apodeme 1S, fig. 16, very similar to that of *anilla* and *millsi*, with the sclerotized bars indicated only by diffuse darkening; the apical margin is scarcely incised on the meson. No definite records of this species have been encountered outside of continental North America. Material previously identified as *fabae* from Argentina was examined and proved to represent four species, *kraemeri*, *tetronis*, *arvalis*, and *loreta*.

Empoasca panisca Ross and Moore

In this species and the next, apodeme 1S is of a peculiar shape found in no other species of the *fabae* complex, fig. 8; the basal bar is stout, the invaginated portion is large and deep but divided completely to the base along the meson, and has no indication of the customary lateral or apical sclerotization. The origin of this peculiar type is somewhat of an enigma but it seems most logical to believe that it arose from a form somewhat like that present in *mexara*, fig. 15.

The latter has a large invaginated portion with almost no sclerotization and a deep central invagination. All other types with a large expanse and a deeply invaginated portion have either lateral, mesal, or apical bars fairly well developed. The depth of sternite 1S in *panisca* seems to indicate that it did not originate from any form in which this structure had already become reduced to the extent found in *loreta*, fig. 11.

This is one of the rarer members of the genus. Since its original description only the two following records have been encountered: Headquarters 15th N. D., Canal Zone, Panama, February 26, 1957, at light, R. M. Altman; and Isla Verde near San Juan, Puerto Rico, May-June 1958, at light, Irving Fox. These two additions increase the known range to Cuba, Puerto Rico, Honduras, and Panama.

Empoasca eccla Ross and Moore

In this species apodeme 1S is exactly like that in *panisca*, fig. 8, substantiating the early belief that the two species are closely related. No material of this species has come to our attention since it was originally described from Panama and Honduras.

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A REVISION OF THE GENUS PHOLEOMYIA IN NORTH AMERICA (DIPTERA, MILICHIIDAE)[1]

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ABSTRACT

The biology of the Milichiidae is briefly summarized, and observations are reported on association of certain *Pholeomyia* species with attine ants. Sixteen species are recognized and keyed; some of these are known presently only from Neotropical areas such as the West Indies, Mexico, and parts of Central America. New species described are *Pholeomyia* **latifrons** (Bahamas), *P.* **poli**, **tifacies** (W. Indies, Mexico to Brazil), *P.* **hurdi** (Mexico)-*P.* **nitidula** (Georgia), *P.* **dampfi** (Central America), and *P.* **texensis** (Texas). Brief diagnoses are given of the other 10 species, their distribution is summarized, and numerous earlier misidentifications are corrected.

The milichiid genus *Pholeomyia* is a well-known genus of small flies, partly because males of many species have a strikingly silvery abdomen and partly because two species, *leucogastra* (Loew) and *indecora* (Loew), are commonly identified in collections. However, little has been known of the species, and most females have not been definitely associated with the distinctive males. Recently, W. L. Brown, Jr., of Harvard University, submitted for identification a female *Pholeomyia* on which he and E. O. Wilson had made an interesting field observation of association with ants. The effort to identify the specimen resulted in a review of available material, discovery of several new species, correction of numerous misidentifications in collections, and recognition of most females in the genus. This paper presents a key to 16 species, descriptions of 6 new species, brief diagnoses of the others, and important corrections on several.

The southern limits of the area covered by this paper are admittedly not well defined. Basically, the study was intended to cover the Nearctic species and those Neotropical species whose ranges overlap the Nearctic. Where material was available from areas adjoining the Nearctic, such as the Bahamas, Cuba, Puerto Rico, and Mexico, it has been included. Insuf-

[1]Accepted for publication October 22, 1958.

ficient material and unavailability of types have made it impossible to review all the Neotropical species, but such review is badly needed. The described Neotropical species, most of which are from Paraguay and Bolivia, appear to be distinct from those included here.

Most of the material recorded here is in the collection of the U. S. National Museum [USNM]. Important collections have also been received through the kindness of J. F. McAlpine of the Canadian Department of Agriculture, C. H. Curran of the American Museum of Natural History [AMNH], W. L. Brown, Jr., of the Museum of Comparative Zoology [MCZ], and Paul D. Hurd of the University of California at Berkeley. I am especially indebted to M. Beier of the Naturhistorisches Museum in Vienna for the loan of two males and two females of Bilimek material of the type species, *Pholeomyia leucozona* Bilimek, and to A. L. Melander of Riverside, California, for the loan of the holotype of *P. myopa* Melander from his personal collection.

BIOLOGY

Malloch (1934, Dipt. Patagonia & S. Chile, Pt. 6, fasc. 5: 461) has summarized the habits of the family by saying that "the larvae of most species feed in manure or decaying vegetable or animal matter." Some adults have been found to feed on the juices of the prey of predacious insects and spiders. Adults of some species of *Milichia*, *Phyllomyza*, and other genera are myrmecophilous. Species of *Milichia* in Africa seem to be closely associated with ants, according to observations by Farquharson (1922, Trans. Ent. Soc. London 1921: 444–447). Adults of *M. proectes* Collin, for example, were observed to "solicit and receive regurgitated food from ants in the track running up the trunk of *Crematogaster*-ant trees" (Poulton, in Collin, 1922, Trans. Ent. Soc. London 1921: 513). Several other species described by Collin at that time were also seen to receive food from the ants.

The observations of Brown and Wilson stimulate speculation as to the relation of the fly and the ant. The specimen of *Pholeomyia*, a female that was subsequently captured and identified as *decorior* Steyskal, was observed at De Leon Springs, Florida, on June 10, 1957, in a grassy roadside strip bordering a dense, moist woods. The fly "was following on the ground close behind a worker of *Trachymyrmex septentrionalis* McCook that was carrying a grass blade. The fly kept a very close and constant distance, about 1 cm. behind the ant, and followed every twist and turn made by the ant. The day was a hot one, and the pace of the ant was rather rapid. When the first attempt to capture the fly was unsuccessful, the fly was disturbed and flew quickly the short distance up to the branch-tip of an herb about 3–5 cm. high. A second *Trachymyrmex* was captured and placed free on the ground near the fly's perch, and the fly pounced down and followed the second ant for a brief period in the same way it had followed the first." "The closeness and tenacity of the fly tracking that little *Trachymyrmex* along the ground" clearly indicated that the ant was being followed. It is possible that the fly, in order to locate an ant nest for oviposition, was following an ant returning from a foraging expedition. I am indebted to Dr. Brown for his kind permission to report the interesting observation.

The type series of *P. texensis*, n. sp. from San Antonio, Texas, "emerged from refuse taken from a nest of the leaf-cutting ant, *Atta texana*," according to information furnished by the collector, E. V. Walter of the Entomology Research Division. A large nest of the ant was excavated, and several species of insects were found in the waste material of the fungus gardens, which is often placed in abandoned cavities, at that time of year (January) often deep in the nest (7–10 feet in the present case). A quantity of the material was placed in jars and held until the insects emerged.

This rearing and the observation of *decorior* following *Trachymyrmex* in Florida suggest some association with fungus-growing ants of the tribe Attini. However, this may be true only of certain species of *Pholeomyia*, because the genus ranges far north of the limit of the fungus-growing ants. Under *P. dampfi*, n. sp., it is recorded that Dampf reared a series (presumed to be conspecific with the type series) from bat dung found far back in caves in Guatemala. Perhaps the apparent myrmecophilous habit of some species is merely a lead to decaying vegetable or animal matter suitable for oviposition.

Pholeomyia Bilimek

Pholeomyia Bilimek, 1867, Verh. Zool.-Bot. Gesell. Wien 17, Abh.: 903. Type-species, *P. leucozona* Bilimek (monotypy).

Rhynchomilichia Hendel, 1903, Wien. Ent. Ztg. 22: 250. Type-species, *Lobioptera argyrophenga* Schiner (orig. desig.) (misident., changed to *R. schineri*, n. sp., by Hendel, 1932, Konowia 11: 137).

Rhynchomilichia: Becker, 1907, Ann. Mus. Nat. Hung. 5: 521.

Pholeomyia (=*Rhynchomilichia*): Hendel, 1911, Wien. Ent. Ztg. 30: 40.

Paramilichia Malloch, 1913, Proc. U. S. Nat. Mus. 46: 130, 135. Type-species, *Milichia longiseta* Becker (monotypy).

Pholeomyia (=*Rhynchomilichia*, =*Paramilichia*): Hennig, 1939, Arb. Morph. Taxon. Ent. Berlin-Dahlem 6: 85.

Pholeomyia: Steyskal, 1943, Ent. News 54: 99–102 (key to N. Amer. species).

Becker (1907) published a revision of the genus, as *Rhynchomilichia*, and included twelve species and two named varieties, eight of the species and the two varieties being new. Eight species and one variety were from Bolivia, Peru, or Paraguay, and are thus out of the range of this paper. Hendel (1911) called attention to the fact that *Pholeomyia leucozona* Bilimek also belonged with this group. For the North American species,

keys were published by Melander (Sept. 1913) for six species (one new) and one variety, and by Malloch (Dec. 1913) for five species. A seventh species was added by Aldrich (1925) and an eighth by Steyskal (1943), the latter giving a key to the males of the eight North American species. All three available keys to the North American species were based entirely or chiefly on the male sex, and for almost all the species it has been considered impossible to identify the females with certainty.

Hendel (1932, Konowia 11: 137) resurrected *Rhynchomilichia* on the character of almost covered, bare lunule, whereas *Pholeomyia* has the lunule visible, with two small bristles. At the same time he noted his misidentification of *argyrophenga*, and changed the type of *Rhynchomilichia* to *R. schineri*, new species (=*argyrophenga* sensu Hendel, 1903, not Schiner). He was followed in this distinction by Malloch (1934, Dipt. Patagonia and S. Chile, Pt. 6, fasc. 5: 461, 462), although the latter did indicate that the character of the lunule seemed rather inadequate. Hennig considered the two synonymous, and I agree. The species show different degrees of exposure of the lunule and of development of a pair of bristles on it.

The species of *Pholeomyia* are uniform for many characters: Head large; front obviously narrower in male than in female, in both usually narrowing slightly toward antennae, smooth, with two rows of interfrontal hairs and sometimes a few others anteriorly, the interfrontal hairs not on definite stripes except in *politifacies*, n. sp.; eye large, occupying most of the head in profile, long axis vertical, hind margin usually not emarginate, only shallowly so in several species; cheek narrower in male than in female, lower margin with a row of strong bristles that ascend anteriorly above the oral margin; antenna short, second segment longer than third, the latter usually small, broader than long; arista slender, base enlarged, flagellum (except in *politifacies*) appearing bare, but minutely pubescent under high magnification. Chaetotaxy: Inner and outer vertical, postvertical, proclinate and divergent ocellar, 3 upper and 3 lower orbital (4–6 lower in *decorior*) pairs of bristles; outer verticals generally strong in female, weaker in male, completely undeveloped only in male *indecora*; anterior upper orbital proclinate in male, lateroclinate or anterolateroclinate in female; one pair of proclinate, usually approximated bristles or bristlelike hairs on lunule, varying from short, weak and scarcely visible to long and strong.

Thorax heavily pollinose, grayish or brownish; mesonotum well covered with hairs. Chaetotaxy: several humeral, 1+1 notopleural, 1 presutural, 1 supraalar, 1 intraalar, 2 postalar, 2–5 dorsocentral, 1–4 or 5 acrostical, and 2 scutellar pairs of bristles; 3 or more strong bristles on mesopleuron; 2 or 3 sternopleural bristles; females generally more strongly bristled and haired on mesonotum than males.

Abdomen, like thorax, heavily pollinose, uniformly dark in females, often ornamented with silvery areas in males, and often broadened and flattened in male; sterna 4 and 5 of male often characteristically beset with bristles and hairs (figs. 6–10); male terminalia (figs. 1–5) rather small and inconspicuous, the ninth tergum with a pair of appendages developed as forceps and differing slightly in shape and size in the various species, the para-anal processes (=cerci of some authors) well developed.

Venation generally as figured for *Milichia leucogaster* [sic] by Williston (1908, Manual N. Amer. Dipt., ed. 3, p. 293, fig. 19). The figure of *Pholeomyia indecora* in Curran's manual (1934, Fam. and Gen. N. Amer. Dipt., p. 337, fig. 19) is that of the broadened wing of female *indecora*; the male wing is longer, the marginal cell is not as broad, and the costal excision is not as deep.

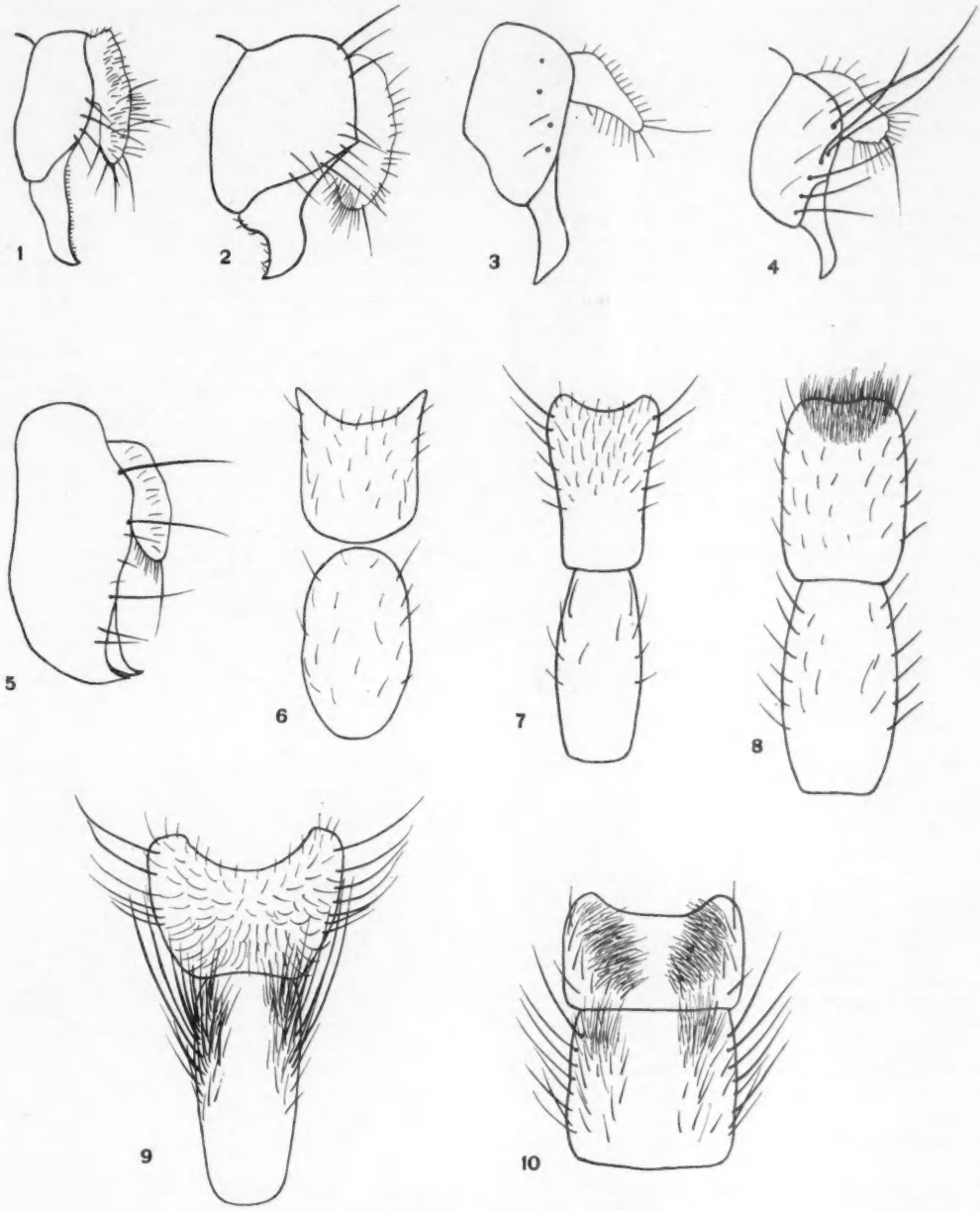
The male terminalia show only slight difference in most species. However, it was discovered that in the males the arrangement of bristles and hairs on the fourth and fifth sterna is very distinctive. Five main kinds, illustrated in figs. 6–10, were observed in the species included in this paper. The largest number of species (six) have the kind shown for *dampfi* (fig. 7), which is only a little different from the plain type in fig. 6, shared by four others. Three species (and possibly *robertsoni* Coquillett) have the distinct kind shown in fig. 9. Figs. 8 and 10 represent unique kinds.

It is interesting to note the character of the mesopleural bristles, because in the past their presence has been recorded but not the number. The typical number in *Pholeomyia* is four strong bristles in a single row. Only *expansa* Aldrich has a greater number, with seven to eight bristles in two irregular rows. Only *indecora* and *latifrons*, n. sp., have three bristles in a single row. While some variation is to be expected in a bristle character, it appears from the considerable material available that the character is remarkably consistent.

KEY TO THE NORTH AMERICAN SPECIES OF PHOLEOMYIA[2]

1. Three to four pairs of dorsocentral bristles, the anterior pair at or close to the mesonotal suture; postvertical bristles parallel to subparallel..... 2
   Two pairs of dorsocentrals, close together on posterior slope of mesonotum; postvertical bristles (except in *decorior*) cruciate at tips, or at least convergent to tips..... 5
2. Antennae, palpi, legs, and halteres yellow (Nicaragua to Argentina).....1. **longiseta** (Becker)
   These structures black or black-brown..... 3

[2]Long series of two new species were received unexpectedly as this paper was in proof, and they have been described in an addendum, with notes on their position in the key. Interesting biological notes accompany one series. Future rearing work in the warm temperate and tropical regions may well reveal a large fauna in this group.



EXPLANATION OF PLATE

Pholeomyia spp.: FIGS. 1–5, male terminalia in side view, showing ninth tergum and left appendage (forceps) and left para-anal process (cercus); FIGS. 6–10, male fourth and fifth sterna.

FIG. 1, *latifrons* (paratype, Rum Cay, Bahamas); 2, *indecora* (Lafayette, Ind.); 3, *leucozona* (Mexico); 4, *dispar* (Rosser, Tex.); 5, *myopa* (Homestead. Fla.); 6, *latifrons* (paratype, Rum Cay, Bahamas); 7, *dampfi* (Petén, Guat.); 8, *leucogastra* (Santiago de las Vegas, Cuba); 9, *dispar* (Rosser, Tex.); 10, *texensis* (paratype, San Antonio, Tex.).

3. Proboscis slender and elongate, the distal section equal to or slightly longer than length of head at vibrissae; face decidedly concave in profile, the epistoma sharply warped forward; male with abdomen dark brown and outer vertical bristles long and strong (Bahamas; ?Cuba) ..... 2. **latifrons,** n. sp.

Proboscis not elongate, distal section obviously shorter than head; face vertical or only weakly concave, the epistoma not strongly warped forward 4

4. Costal excision deep, two or more times the length of fore crossvein, longer in female than in male; mesopleuron with three bristles in a single row along posterior margin; wing light brownish tinted; male with abdomen dark brown and outer vertical bristles absent (present in female) (widespread, Canada and U. S., especially eastern) ..... 3. **indecora** (Loew)

Costal excision shorter, only 1.5 times the length of fore crossvein; mesopleuron more heavily bristled, typically with seven bristles in two rows; wing whitish; male with dorsum of abdomen silvery except for narrow first tergum, and outer vertical bristles long and strong (Calif.) .. 4. **expansa** Ald.

(Only the male is known to me, but the first three characters are common to both sexes in the other species examined and undoubtedly characterize female *expansa.*)

5. Face polished black; arista sparsely but distinctly pubescent, the hairs at least as long as diameter of enlarged base of arista (West Indies, Centr. Amer., Brit. Guiana, Brazil) .5. **politifacies,** n. sp.

Face leaden-gray pollinose, subshining; arista apparently bare, microscopically pubescent under high magnification 6

6. Proboscis slender and elongate, the distal section obviously longer than head; face concave in profile, the epistoma conspicuously warped forward . 7

Proboscis of short to moderate length, the distal section clearly shorter than head; face vertical or nearly so, the epistoma not strongly warped forward 8

7. Postvertical bristles parallel to subparallel; apex of ocellar triangle, immediately anterior to median ocellus, usually with a pair of short, approximated, proclinate and divergent bristles; 4–6 pairs of strong, mesoclinate lower orbital bristles; male abdomen dark brown (southeastern U. S.) ..... 6. **decorior** Steys.

Postvertical bristles cruciate at tips or convergent; apex of ocellar triangle without bristles; 3 pairs of lower orbitals, interspersed with fine orbital hairs; dorsum of male abdomen silvery on segments 2 through 5 (Mexico) ..... 7. **hurdi,** n. sp.

8. Males 9

Females (unknown for *nitidula* and *robertsoni,* and somewhat doubtful in the species near *leucogastra.*) 17

(Males)

9. Dorsum of abdomen, except first tergum and distal half of fifth, densely covered with rusty reddish, appressed pubescence and pollen; mesonotum heavily brown pollinose (Fla. to Brazil) ..... 8. **myopa** Mel.

Dorsum of abdomen marked with some areas of silvery pollen 10

10. Silvery areas confined to sides of fifth tergum, a narrow median stripe and apex dark brown, concolorous with rest of abdomen; calypteres brown; wing hyaline, brownish tinted; (Md. to Fla.) ... 9. **pseudodecora** (Beck.)

Abdominal segments 2 to 5 with some silvery areas on terga; wing and calypteres often whitish 11

11. Dorsal aspect of terga 2 to 4 entirely silvery, or at most with small median brown triangle at base of second, and each with a single row of black, well-spaced, hairlike bristles along posterior margin, the second tergum in one species with 6 to 8 additional scattered hairs on mesal third 12

Dorsal aspect of tergum 2, or each of terga 2 to 4, with broad, black or brown mesal area 15

12. Wing distinctly whitish; calypteres white; dorsum of fifth tergum almost entirely silvery, only a narrow black band distad to the row of marginal bristles; front velvet black posteriorly, often narrowly reddish anteriorly; second tergum with single row of bristles along posterior margin 13

Wing hyaline, brownish tinted; calypteres brown, at least on outer margin; dorsal aspect of fifth tergum broadly black at apex, the remainder silvery; front brown to black 14

13. Sternopleuron with 5–7 erect, strong, bristle-like hairs and bristles; fifth abdominal sternum posteriorly with a dense patch of fine hairs, the fourth sternum sparsely bristled (fig. 8) (Cuba, Mexico) ..... 10. **leucogastra** (Loew)

Sternopleuron typically with only three bristle-like hairs and bristles, an occasional additional one weak and inconspicuous; fifth abdominal sternum not with dense posterior patch of hairs, but fourth sternum with moderately dense posterolateral areas of long hairs and bristles (fig. 9) (southern U. S.) ..... 11. **dispar** (Beck.)

14. Second abdominal tergum with a group of 6–8 well-spaced black setae on mesal third of segment, in addition to row along posterior margin; mesonotum, viewed from behind, appearing very dark brown to blackish; anterior dorsocentral bristle long and strong, over three-fourths the length of posterior doroscentral, and farther from it than it is from nearest acrostical; front long and narrow, the length 1.66 times the width at vertex; fourth and fifth sterna similar to those of *dispar* (cf. fig. 9), the fourth with posterolateral areas of long hairs and bristles (Ga.) ..... 12. **nitidula,** n. sp.

Second abdominal tergum with only one row of well-spaced, black, hairlike bristles along posterior margin; mesonotum brownish pollinose, but viewed from behind appearing bluish-gray to greenish-gray pollinose; anterior dorsocentral bristle relatively short, half the length of posterior bristle and separated from it by slightly less than distance from latter to nearest acrostical bristle; front relatively broad and short, the length 1.25–1.30 times the width at vertex; fourth and fifth sterna (fig. 7) sparsely bristled (Guatemala, Mexico ..... 13. **dampfi,** n. sp.

15. Second tergum with few hairs, about one irregular row in addition to that along posterior margin; third and fourth terga extensively brown in dorsal aspect, the brown spot on third forming a large triangle with its broad base on posterior margin, the fourth brown on posterior half to two-thirds, silvery anteriorly and on sides; fifth tergum sparsely haired, only one row of six hairs and a scattered hair or two anterior to the posterior marginal row of bristles (Fla.) ..... 14. **robertsoni** (Coq.)

Second tergum with numerous hairs in about 2–3 irregular rows, almost the full width of tergum, in addition to the row of hairlike bristles along posterior margin; third and fourth terga usually entirely silvery; fifth tergum rather densely haired, with 4–5 rows covering most of surface .. 16

16. Hind margin of eye, about midway, distinctly although shallowly emarginate; second tergum with about three irregular rows of hairs, the third and fourth each with two rows; fifth tergum almost entirely silvery; mesonotum and scutel-

lum, viewed from behind, bluish-gray to greenish-gray pollinose; fourth and fifth sterna as in fig. 10, with dense lateral areas of fine hairs (Texas) . . 15. **texensis**, n. sp.

Hind margin of eye straight, not at all emarginate; second tergum with more numerous hairs, in about six irregular rows, the third and fourth each with a single row, along the posterior margin; fifth tergum chiefly black, silvery pollinose basally; mesonotum and scutellum, viewed from behind, definitely brown to brownish-gray pollinose; fourth and fifth sterna as in *dampfi* (cf. fig. 7), without conspicuous patches of fine hairs (Mexico) . . . . . 16. **leucozona** Bilimek

(Females)

(Unknown for *nitidula* and *robertsoni*)

17. Front, mesonotum, and scutellum concolorous, distinctly yellowish-gray pollinose, in strong contrast to the dark brown abdomen; wing brownish tinted . . . . . 8. **myopa** Mel.

Mesonotum and scutellum brown to brownish-gray pollinose, in a few species bluish- or greenish-gray when viewed from behind; front brown to blackish, sometimes reddish anteriorly, but never yellow-gray pollinose 18

18. Cheek narrow but distinct, equibroad throughout its length, and not linear, half or more the greatest breadth of a palp 19

Cheek narrowing posteriorly, at one place virtually linear, only one-fourth to one-fifth the breadth of a palp; wing and calypteres brownish tinted . . 22

19. Front relatively broad and short, the width at vertex equal to length, often giving the illusion of being wider than long 20

Front obviously longer than broad, the width at vertex 0.81 to 0.88 times the length 21

20. Interfrontal hairs minute and inconspicuous, not set on definite plate; sternopleuron with 5–7 erect, strong bristlelike hairs in addition to the three bristles (Cuba, Mexico) . . . . . 10. **leucogastra** (Loew)

Interfrontal hairs coarser and more conspicuous, usually appearing set on distinct though incomplete, linear interfrontal plate; sternopleuron with 3 bristles; hind margin of eye, about midway, distinctly although shallowly emarginate (Texas) . . . . . 15. **texensis**, n. sp.

21. Wing whitish, especially on alula and anal areas; calypteres white (southeastern U. S.) . . . . . 11. **dispar** (Beck.)

Wing brownish tinted; calypteres brownish, especially on outer side (Md. to Fla.) . . . . . 9. **pseudodecora** (Beck.)

22. (Females of *leucozona* Bilimek and *dampfi*, n. sp., come here. The two available specimens of the former are unfortunately too poor to be compared satisfactorily with the type series of *dampfi*, but females of the two species are unquestionably very close. It is possible that the large third antennal segment of female *dampfi* will be a useful character, but lack of antennae on the available females of *leucozona* makes it impossible to tell at this time.)

1. **Pholeomyia longiseta** (Becker)

Milichia longiseta Becker, 1907, Ann. Mus. Nat. Hung. 5: 530 (Paraguay).

Paramilichia longiseta: Malloch, 1913, Proc. U. S. Nat. Mus. 46: 135 (Nicaragua).

Pholeomyia longiseta: Hennig, 1939, Arb. Morph. Taxon. Ent. Berlin-Dahlem 6: 86 (redescribed).

Diagnosis.—Front grayish-yellow pollinose; postverticals subparallel or slightly divergent; anterior pair of interfrontals proclinate, as strong as lower orbitals; face weakly concave, the epistoma not projecting in profile; cheek broad, nearly equal to breadth of third antennal segment; proboscis short. Thorax and abdomen concolorous in both sexes, grayish pollinose, the mesonotum more or less yellowish gray and the scutellum partly brownish gray; four pairs of dorsocentral bristles. Abdomen not dissected, but fifth sternum of male appears to be much like that of *latifrons* (cf. fig. 6), but with longer posterolateral bristles. Wing and calypteres brownish; costal excision deep, twice the length of fore crossvein.

In addition to the specimen from Nicaragua recorded by Malloch [USNM], I have seen material from the Argentine provinces of Formosa and Chaco, adjoining Paraguay [Inst. Miguel Lillo, Tucumán, Argentina]. Malloch's specimen is badly broken, but apparently belongs to this species. All agree with Hennig's redescription based on specimens from Paraguay.

The species stands out strongly in the genus *Pholeomyia* because of its yellow antennae, palpi, legs and halteres, all of which are black or black-brown in the other known species. With this habitus, it is not surprising that a distinct genus was proposed for it. However, the structural characters are typical of *Pholeomyia*, and I agree with Hennig in placing it there. It is definitely Neotropical, but is included here because it may range into the area covered by this review.

2. **Pholeomyia latifrons,** new species

(Figures 1, 6)

Near *indecora*, with three pairs of dorsocentral bristles and concolorous thorax and abdomen in male, but with broader front and strong outer vertical bristles, and both sexes with broader cheek, elongate proboscis, and concave face with epistoma strongly warped forward.

Male.—Black to black-brown; cheek reddish brown; veins yellow; wing distinctly whitish; calypteres white; thorax and abdomen concolorous, brownish-gray pollinose.

Front broad, wider than an eye, at the vertex 0.45 and at lunule 0.40 times the width of head; postvertical bristles parallel or subparallel; outer verticals long and strong, subequal to inner verticals and postverticals; lunular bristles moderately strong; face concave, gray pollinose, the epistoma well warped forward and visible in profile; parafacial broad, clearly evident in profile; cheek relatively broad for the genus, 0.15 times the height of head and equal to breadth of third antennal segment; proboscis elongate, distal section longer than the head.

Mesonotum with three pairs of long, strong, well-spaced dorsocentral bristles, the anterior opposite the ends of mesonotal suture; two pairs of acrostical bristles far back on posterior slope of mesonotum, the anterior weak; mesopleuron with three strong bristles in a single row. Abdomen with terga 2–5 rather densely beset with

short black hairs, except for narrow band along anterior margin of each tergum; sterna 4 and 5 simple, sparsely beset with short hairs (fig. 6); terminalia (fig. 1) with long forceps and para-anal processes.

Wing venation as in *indecora*; costal excision short, not as long as fore crossvein, the anterior bristle, on lappet above the excision, prominent, longer than fore crossvein.

Female.—Similar to male in general habitus, differing in sterna, terminalia and following characters: Front broader, obviously wider than an eye, and slightly over half the width of head; cheek slightly wider than in male, 0.18–0.20 times the height of head; wing broader than in male, the subcostal and marginal cells conspicuously broadened, although not as extreme as in *indecora*.

Length of body, 3 mm.; of wing, 2.75 mm.

Holotype male and allotype, Governor's Harbour, Eleuthera Island, Bahama Islands, Mar. 31, 1953 (E. B. Hayden), in the American Museum of Natural History. Paratypes, 21 ♂♂, 5 ♀♀, Bahama Islands, collected by E. B. Hayden, L. Giovannoli, and G. B. Rabb on the Van Voast-American Museum of Natural History Bahamas Expedition. The paratypes represent a scattering of localities on San Salvador, Fortune, Mayaguana, and New Providence Islands, the Turks and Caicos Islands, and Rum, Fish, North, and Abaco Cays, Feb. 4 to May 10, 1953 [AMNH and USNM].

Eight other specimens (4 ♂♂, 4 ♀♀) from the Bahamas Expedition are not in good condition and have not been considered paratypes. The only additional localities are The Bight and Bennett's Harbour, Cat Island, Mar. 22 and 24, respectively.

This species is close to *indecora*, with three pairs of dorsocentrals, parallel postverticals, brown-black male abdomen, and only three bristles on the mesopleuron. Males of the two can readily be separated by the broader front and strong outer vertical bristles of *latifrons*, and by the male terminalia (cf. figs. 1, 2). Females are more difficult to distinguish, but the decidedly longer proboscis and projecting epistoma of *latifrons* enable one to recognize it. Further useful characters are the broader parafacial and whitish wing and calypteres of *latifrons*. Females of *indecora* are also more heavily bristled, with 4–5 pairs of dorsocentrals.

I know of no mainland records of *latifrons*, but it may well occur, at least occasionally, in southeastern United States. Any presumed *indecora* from that area should be carefully checked.

One male, Havana, Cuba (C. F. Baker) [USNM] probably belongs here, but may represent another species. The mesopleuron has three smaller bristles in two rows between the two large lower bristles, and the costal excision of the wing is slightly more pronounced, but I can find no other differences. The male terminalia are like those of *latifrons*. For the present, I regard it as a variant of *latifrons*.

3. **Pholeomyia indecora** (Loew)

(Figure 2)

Lobioptera indecora Loew, 1869, Berl. Ent. Ztschr. 13: 50 (Centuria 8, no. 94) (Nebr.).

Lobioptera indecora: Coquillett, 1900, Proc. U. S. Nat. Mus. 22: 268 (N. H. to Ga.; for the Vieques Island record, however, see *politifacies*).

Milichia indecora: Baker, 1904, Invertebrata Pacifica 1: 26 (Ormsby Co., Nev.).

Rhynchomilichia indecora: Becker, 1907, Ann. Mus. Nat. Hung. 5: 523.

Pholeomyia indecora: Melander, 1913 (Sept.), Jour. New York Ent. Soc. 21: 238 (N. H. to Fla. and west to Nebr. and Idaho; the West Indies record is probably based on Coquillett, 1900, for which see *politifacies*).

Pholeomyia indecora: Malloch, 1913 (Dec.), Proc. U. S. Nat. Mus. 46: 134 (N. H to Ga. and Texas; the Vieques Island record belongs under *politifacies*, and the Tabasco, Mexico, specimen is *myopa*).

Diagnosis.—Thorax and abdomen concolorous in both sexes, black, gray to grayish-brown pollinose. Postvertical bristles parallel or subparallel; outer vertical bristles strong in female, undeveloped in male; cheek relatively broad for the genus, in female nearly as broad as the third antennal segment, narrower in male; front of male much narrower than an eye, at the narrowest slightly over one-fourth the width of head; face weakly concave, gray pollinose; proboscis short. Three to five pairs of dorsocentral bristles, stronger in female than in male; mesopleuron almost always with three strong bristles in a single row. Wing hyaline, light brownish; calypteres brownish; costal excision deep, two or more times the length of fore crossvein; wing in female notably shorter and broader than in male, the marginal cell strikingly broadened, and costal excision longer than in male. The male terminalia (fig. 2) show broader and stouter forceps than the other species. The fourth and fifth abdominal sterna of the male are like those of *latifrons* (cf. fig. 6), sparsely beset with short hairs.

Approximately 240 specimens are before me, from Calif., Conn., D. C., Ga., Idaho, Ill., Ind., Iowa, Kans., Maine, Md., Mass., Mich., Nebr., Nev., N. H., N. J., N. Y., N. C., Penn., Vt., Va. in the United States, and from Alta., B. C., N. S., Ont., Quebec, and Sask. in Canada. I have also studied the holotype in the Museum of Comparative Zoology. Far western records are few: Fallen Leaf, Lake Tahoe, Calif.; Moscow and Montpelier, Idaho; Ormsby Co., Nev.; Victoria, Comex, and Squamish, B. C.

This is the most common, or at least most often-collected species of the genus. In eastern North America it is the only known species with three pairs of dorsocentral bristles. In the west, *P. expansa* must be considered, but *indecora* is easily distinguished by the black-brown abdomen of the male and by the fewer mesopleural bristles in both sexes. In the southeastern states, *lati-*

frons from the Bahamas must be considered a possible immigrant. Misidentifications have been numerous in the past, and no less than six different species have been found in collections identified as *indecora*, most of these being the drab females which lack striking characters.

P. indecora has been recorded several times from Puerto Rico, but I doubt that it occurs there. The published records that I have been able to recheck belong elsewhere (Vieques Island specimen, by Coquillett, 1900 = *politifacies*; Caguas and Barceloneta specimens, by Wolcott, 1936 = *myopa*; Mayaguez and Mona Island specimens, by Curran, 1928 = *myopa*; and other available West Indian specimens are not *indecora*). The published records of *indecora* from Jamaica are also probably erroneous; however, the material on which they were based has not been examined (Johnson, 1919, Bull. Amer. Mus. Nat. Hist. 41: 449; Gowdey, 1927, Cat. Ins. Jamaica, p. 89).

4. **Pholeomyia expansa** Aldrich

Pholeomyia expansa Aldrich, 1925, Proc. U. S. Nat. Mus. 66 (Art. 18): 1 (Mt. Lowe, Calif.).

Diagnosis (male).—Thorax and narrow first abdominal tergum black, thinly brownish pollinose, the remaining terga brilliant silvery. Postvertical bristles parallel to slightly divergent; outer verticals strongly developed, subequal to inner verticals; cheek narrow, but wider than haustellum; proboscis not unusually elongate, distal section obviously much shorter than length of head; face weakly concave; front broader than usual in male, at vertex two-fifths and at lunule one-third the width of head. Four pairs of dorsocentrals; mesopleuron strongly bristled, with 7–8 bristles in two irregular rows. Abdominal sterna 4 and 5 sparsely beset with hairs, as in *latifrons* (cf. fig. 6), sternum 5 about as figured but sternum 4 much reduced, little over one-fifth the width of 5. Wing conspicuously whitish; calypteres dark brown; costal excision shorter than in *indecora*, only 1.5 times the length of fore crossvein.

I have seen only the holotype and seven paratypes, all males [USNM].

Although only the male is known to me, the first three characters used for *expansa* in the key are common to both sexes in other species of *Pholeomyia* and undoubtedly serve for the female of *expansa* as well. The broad, silvery abdomen is a striking feature. The other species in the group with 3–4 pairs of dorsocentrals, *indecora* and *latifrons*, have the male abdomen entirely brown-black, concolorous with the thorax.

5. **Pholeomyia politifacies,** new species

Small gray species with face predominantly polished black, and arista long pubescent.

Female.—Black, the wing and calypteres whitish; front subshining black, contrasting with the gray pollinose orbits, ocellar triangle, and linear interfrontal stripes; body subshining, the thorax bright gray pollinose, seen from behind a faint bluish or greenish gray; abdomen black-brown pollinose.

Front broad, at vertex almost half the width of head, narrowing slightly towards antennae; postvertical bristles cruciate at tips; outer verticals well-developed; each row of interfrontal hairs set on a linear plate, reminiscent of *Desmometopa*; posterior margin of eye, about midway, with a slight but perceptible indentation; face concave, smooth and polished, a little gray pollen dorsally near antennal bases; cheek narrow; proboscis not greatly elongated, the distal section shorter than head; arista distinctly pubescent, the hairs at least as long as diameter of enlarged base of arista.

Thorax with two pairs of dorsocentral bristles, the anterior short and weak, half or less than the length of posterior, and close to it, the distance between the two dorsocentral bristles less than the distance from posterior dorsocentral to a prescutellar acrostical bristle; mesopleuron with four strong bristles in a single row. Wing not conspicuously shortened and broadened as is often the case in the female sex; costal excision short.

Length of body, 1.75 mm.; of wing 2 mm.

Holotype female, Cambito, Prov. Trujillo, Dominican Republic, Dec. 22, 1955 (J. Maldonado Capriles). Type No. 64303 in the U. S. National Museum, deposited by courtesy of the collector. Paratypes, all females: Vieques Island, Puerto Rico, Feb. 1899 (August Busck) [recorded as *Lobioptera indecora* Loew by Coquillett, 1900, Proc. U. S. Nat. Mus. 22: 268]; near Marine Hotel, Barbados, Sept. 14, 1918 (H. Morrison); Turrialba, Costa Rica, March 1954, light trap (C. H. Batchelder) [all, USNM]; two females, La Caja, near San José, Costa Rica, 1930 (H. Schmidt) [Deut. Ent. Mus.].

A series of about 65 specimens, all females, Mayaguez, Puerto Rico, Mar. 30, 1950 (H. E. Warmke), collected at flowers of *Hevea brasiliensis* [USNM], is unfortunately in too poor condition to be included in the type series. It does demonstrate the consistency of the characters upon which the new species is founded, and it indicates that the species is probably fairly common, although small and inconspicuous. Two damaged females are also available from near Georgetown, British Guiana, Sept. 22, 1918 (H. Morrison) [USNM].

I have seen four males referable to *politifacies*, two each from Higuito, San Mateo, Costa Rica (Pablo Schild), and from Tocantins, Alcobaca River, Pará, Brazil, Dec. 6, 1926 (E. G. Holt) [USNM]. The Costa Rica specimens are in poor condition. The Brazil specimens are in fair condition, but because the locality is so far distant from the type locality I have not included them in the type series. The front is strongly narrowed anteriorly, as usual in males, and the face is

narrow. The linear interfrontal stripes so evident in the females are weak and not continuous, with traces showing near the bases of the hairs. The cheek is linear. The facets in the anterior half of each eye are distinctly enlarged. The outer vertical bristles are shorter than in the female, but are still distinct. The polished face is sometimes difficult to see in the male because the face is narrow and often hidden by the antennae. Abdominal sterna 4 and 5 are like those of ***dampfi*** (cf. fig. 7). The male terminalia resemble those of ***leucozona*** (cf. fig. 3), but the posteroapical angle of the forceps is more rounded and the forceps appears less "boot-shaped."

I have seen a few specimens of what appears to be this species from Mataiea, Tahiti, Society Islands (Mumford and Adamson) [Bishop Museum, Honolulu].

6. **Pholeomyia decorior** Steyskal

Pholeomyia decorior Steyskal, 1943, Ent. News 54: 100 (Brunswick Co., N. C.).

This species was originally described as having very narrow silvery fasciae on the anterior margins of second to fourth terga. However, the appearance is deceiving; actually there are no silvery fasciae, and the abdomen is entirely black, brownish pollinose and subshining. The species is still valid, and the unicolorous abdomen in the male is unique among the known North American species having only two pairs of dorsocentrals. Only ***indecora*** and ***latifrons***, both with three pairs of dorsocentrals, have an entirely black-brown abdomen in the male. The habitus is much like that of ***indecora*** Loew, which has three pairs of dorsocentral bristles.

Except for the above correction, the species has been adequately described by Steyskal. The diagnostic characters are as follows: Thorax and scutellum concolorous in both sexes, black, subshining, thinly brown pollinose; postvertical bristles subparallel to slightly divergent; outer verticals well developed in both sexes; 4–6 pairs of lower orbitals, convergent to cruciate at tips; apex of ocellar triangle, immediately anterior to median ocellus, typically with a pair of approximated, proclinate and divergent, bristly hairs; cheek linear in male, slightly wider in female; face gray pollinose, concave in profile, the epistoma conspicuously warped forward; proboscis slender, elongate and geniculate, both distal section and haustellum as long or longer than the head. Dorsocentral bristles in two pairs. Wing brownish tinted; calypteres white. Females may be recognized by the same combination of characters as the males. Abdominal sterna 4 and 5 are like those of ***dampfi*** (cf. fig. 7).

I can record only eight specimens besides the male holotype: Female, "N. C."; female, DeLeon Springs, Fla., June 10, 1957 (E. O. Wilson, W. L. Brown, Jr.); male, Levy Co., Fla., Mar. 7, 1954 (H. V. Weems, Jr.); female, Alachua Co., Fla., Mar. 18, 1956 (R. A. Morse) [all USNM]; female, Tifton, Ga., July 18, 1896 [Sabrosky Colln.]; female, Atco., N. J., June 6 (C. W. Johnson) [MCZ]; female, Jacksonville, Fla., (Mrs. A. T. Slosson) [AMNH]; female, Gainesville, Fla., Apr. 25, 1952 (O. Peck) [Canad. Dept. Agr.]. The holotype is now deposited in the U. S. National Museum.

The New Jersey specimen was recorded as ***Rhynchomilichia indecora*** by Johnson (1910, Diptera, in Smith, Insects of New Jersey, Ann. Rept. N. J. State Mus., p. 813). The other records of ***indecora*** in that list are correct. The Jacksonville, Fla., specimen is probably that recorded as ***indecora*** by Johnson (1913, Bull. Amer. Mus. Nat. Hist. 32: 89). The North Carolina specimen was determined as ***indecora***, probably by Coquillett.

P. decorior possesses two characters that are unique in the group with two pairs of dorsocentral bristles, namely the subparallel postverticals, and the larger number of strong anterior orbitals. In that group it also differs from all but ***hurdi*** in the projecting epistoma and slender and elongate proboscis. Another unique character, the pair of bristly hairs at the apex of the ocellar triangle, is present in seven of the eight available examples, and in the holotype, and is probably typical although occasionally variable.

7. **Pholeomyia hurdi,** new species

Species superficially like ***leucogastra***, with two pairs of dorsocentral bristles and dorsum of abdomen predominantly brilliant silvery, but the proboscis slender and elongate, face concave, and epistoma projecting.

Male.—Predominantly black; front dull black, the orbits and lunule subshining; thorax quite shining though finely dark gray pollinose; scutellum duller, with brownish pollinosity; abdominal terga 2 through 5 brilliant silvery except for narrow apical margin of 5, distad of the submarginal row of bristles; wing hyaline or whitish hyaline with yellow veins; calypteres white.

Front appearing relatively narrow, at vertex slightly over one-third width of head but strongly narrowing to one-fifth the head width measured at the lunule; lunule conspicuously subquadrate, the dorsal margin straight, the surface with a weak pair of hairs; postverticals strongly cruciate; outer verticals strong, equal to postverticals; eye large, facets of anterior two-fifths moderately enlarged, the hind margin straight; face pollinose, concave, the epistoma well warped forward and very evident in profile; parafacial and cheek linear; proboscis slender and elongate, the distal section and haustellum each well over the length of head; third antennal segment relatively small; arista minutely pubescent.

Mesonotum with two pairs of dorsocentral bristles, the anterior strong but only two-thirds the length of posterior, and set closer to the

posterior than the latter is to the prescutellar acrostical bristle, the latter as long and strong as a posterior dorsocentral; intrapostsuturals not developed, so the dorsocentral and acrostical bristles stand out as long and strong bristles surrounded by short, appressed clothing hairs; mesopleuron with four bristles in a single row; sternopleuron with a single thick bristle, preceded by a weak hairlike bristle only a little longer than the hairs.

Abdominal terga almost devoid of hairs and bristles, the second through fourth each with a row of short, well-separated black bristles along posterior margin, the fifth with a submarginal row of longer bristles, with a few short hairs interspersed; terga 2–5 of approximately equal length, but in most specimens telescoped by drying or because of immaturity so that the length of second tergum is often twice the combined lengths of 3 and 4; sterna 4 and 5 like those of *dampfi* (cf. fig. 7); male terminalia near *dispar* (cf. fig. 4), the forceps slender but shorter than in *dispar*.

Wing venation ordinary for the genus; costal excision short.

Female.—As described for male, except for terminalia and as follows: Front broader, at the vertex wider than an eye and nearly two-fifths the width of head, almost parallel-sided, narrowing only slightly and at lunule measuring one-third the head width; face correspondingly broad; eye facets uniform in size. Abdomen black, quite shining though finely brownish pollinose, the entire dorsum beset with hairs.

Length of body and of wing, 2.75 mm.

Holotype male and allotype, Ahuacatlan, Nayarit, Mexico, July 18–22, 1951 (P. D. Hurd), in the collection of the California Academy of Sciences. Paratypes: 7 males, 4 females, same data as holotype; 4 males, 1 female, 15 km. N. of Chapalilla, Nayarit, Mexico, July 19, 1951 (Hurd); 1 female, 4 mi. W. of El Cercado, Nuevo Leon, Mexico, June 6, 1951 (Hurd); 1 female, Guadalajara, Jalisco, Mexico, July 23, 1951 [Calif. Acad. Sci. and USNM]. The allotype and five topotypical paratypes were taken at flowers of *Donnellsmithia Hintonii* M. & C.; four of the Chapalilla series were labeled "*Baccharis*," and the Guadalajara female "*Baccharis glutinosa*." Six other specimens from Chapalilla and Guadalajara are somewhat damaged and are not included in the type series.

Although it resembles *leucogastra* in the color of the male abdomen, the elongate proboscis and projecting epistoma mark *hurdi* as distinct from all species considered in this paper except *decorior* and *latifrons*, which are quite different on other characters.

I am pleased to name this species after the collector, who has secured fine series of many interesting Diptera on this and other collecting trips.

8. **Pholeomyia myopa** Mel.

(Figure 5)

Pholeomyia myopa Melander, 1913, Jour. New York Ent. Soc. 21: 238 (Haiti).

Diagnosis, male.—Front fine-grained, velvety brown; mesonotum and scutellum brownish pollinose; abdomen, except first tergum and distal half or three-fifths of fifth, rusty reddish; wing and calypteres brown. Front narrow, at the vertex 0.30 times the width of head, narrowing to 0.15 at the lunule; postverticals cruciate; outer verticals present, but short and hairlike; face nearly vertical, the epistoma not projecting; cheek linear; proboscis short. Mesonotum with two pairs of dorsocentral bristles; mesopleuron with four strong bristles in a single row. Sterna 4 and 5 of abdomen as in *dampfi* (cf. fig. 7); terminalia (fig. 5) characteristic, with greatly enlarged ninth tergum. Length, 3 mm.

Female.—Front, mesonotum and scutellum concolorous, yellowish-gray pollinose; abdomen dark brown to brown-black, subshining; wing and calypteres paler than in male, the former yellowish to light brown, the latter yellowish white. Front narrower than usual in female *Pholeomyia*, at the vertex 0.36 times the width of head, narrowing slightly toward antennae; outer vertical bristles long and strong.

Distribution.—Besides the type from Haiti, I have before me 45 specimens from Florida (Homestead, Key West, Key Largo, Stock Island, and Monroe County), the Bahamas (Darby, New Providence, and Grand Bahama Islands), Cuba (Guantanamo), Dominican Republic (Ciudad Trujillo, San Pedro de Macoris, and two localities in Prov. Trujillo), Puerto Rico (Mona Island, Lajas, Caguas, Barceloneta, Rio Piedras, and Mayaguez), Mexico (Tabasco), Costa Rica (San Mateo), Panama Canal Zone (Camaron), Venezuela (San Esteban), Trinidad (Maracas Valley), and Brazil (Tapajos in Pará).

The specimen from Mexico [USNM] was recorded as *indecora* by Malloch (1913, Proc. U. S. Nat. Mus. 46: 134), the specimens from Mayaguez and Mona Island, Puerto Rico [AMNH], as *indecora* by Curran (1928, Scient. Survey Porto Rico and Virgin Is. 11(1): 68), and the specimens from Caguas and Barceloneta, Puerto Rico [USNM], as *indecora* by Wolcott (1936, Insectae Borinquenses, Puerto Rico Univ. Jour. Agr. 20: 392).

I am indebted to Dr. Melander for the loan of the holotype, which enabled me to confirm the identify of my material and to ascertain that it has only two pairs of dorsocentral bristles instead of three as originally stated. The apparent third pair of dorsocentrals is intrapostsutural, each bristle of the pair set between and slightly in advance of the posterior dorsocentral and posterior acrostical bristles. In the male sex, the species is unique in the genus in having the dorsum of the abdomen chiefly rusty reddish. The fe-

males that appear to be associated differ markedly from the male in the color of the front and thorax, but they are consistently associated by locality and by the fact that neither sex can be matched with any other available species. It is concluded, therefore, that the species is sexually dimorphic in the color of front and thorax as well as in the normally dimorphic appearance of the abdomen. The male terminalia (fig. 5) are unique among the species that I have examined.

9. **Pholeomyia pseudodecora** (Becker)

Rhynchomilichia pseudodecora Becker, 1907, Ann. Mus. Nat. Hung. 5: 524, pl. 12, fig. 6 (Tifton, Ga.).
Pholeomyia pseudodecora: Melander, 1913, Jour. New York Ent. Soc. 21: 238.

Diagnosis.—Front velvet black, reddish on anterior fourth to third: thorax and abdomen black-brown, dark brown pollinose, concolorous in both sexes except for distal portion of male abdomen, in which the fifth tergum is silvery except for narrow median stripe and apex, and the extreme sides of third and fourth terga are obscurely silvery-gray; wing brownish tinted; calypteres brown.

Front at narrowest one-fourth the head width in male, two-fifths in female; postverticals cruciate; outer verticals long and strong in female, very short and hardly noticeable in male; face gray pollinose, weakly concave, epistoma not strongly projecting; cheek linear in male, narrow in female; proboscis not elongate, distal section shorter than head. Two pairs of dorsocentral bristles; mesopleuron with four strong bristles in a single row. Abdomen not dissected in the limited material, but sterna 4 and 5 approximately as in *dispar* (cf. fig. 9), the lateral areas on 4 less dense.

Distribution.—I have seen only two males of this species: Augusta, Ga., Apr. 5, 1946 (P. W. Fattig), and Alachua Co. Fla., Oct. 21, 1956 (R. A. Morse) [USNM]. In addition, there are five females which I identify as *pseudodecora*: Augusta, Ga., same data as male noted above; 2, Tifton, Ga., 1896 (previously identified as *indecora*); Bladensburg, Md., Oct. 2, 1914 (R. C. Shannon) [all, USNM]; Alachua Co., Fla., Aug. 12, 1955 (R. A. Morse) [Fla. State Plant Board Colln.].

Becker's figure of the male abdomen makes identification of this species very easy. However, he described the calypteres as whitish, whereas they are brown, or at least brown-margined, in the only males before me. He probably also had female *leucogastra* confused here, because he described the female wing as "somewhat whitish." It may also be noted that the extreme sides of the third and fourth terga are narrowly and obscurely silvery, although this was overlooked by Becker, who described only the dorsal aspect.

If I have correctly associated the females, *pseudodecora* and *leucogastra* are very close in that sex, and can easily be confused. From comparison with the males, I have placed those females with whitish wing and calypteres as *leucogastra*, and those with brownish wing and calypteres as *pseudodecora*. The small series of each available for study makes it impossible to do more than make a tentative association at this time.

10. **Pholeomyia leucogastra** (Loew)

(Figure 8)

Milichia leucogastra Loew, 1861, Wien. Ent. Monatschr. 5: 43 (Cuba).
Lobioptera leucogastra: Loew, 1869, Berlin. Ent. Ztschr. 13: 50 (Centuria 8, no. 95).
Rhynchomilichia leucogastra: Becker, 1907, Ann. Mus. Nat. Hung. 5: 523.
Pholeomyia leucogastra: Melander, 1913, Jour. New York Ent. Soc. 21: 238.

Diagnosis.—Front velvet black, reddish on anterior fourth to third; abdomen of male brilliant silvery, only the first tergum and narrow distal margin of fifth black; abdomen of female concolorous with thorax; wing and calypteres conspicuously whitish. Postvertical bristles cruciate; outer verticals present in both sexes, though short and weak in male; face gray pollinose, weakly concave; cheek linear in male, slightly wider in female; proboscis not elongated, distal section obviously shorter than head. Two pairs of dorsocentral bristles; mesopleuron with four strong bristles in a single row; sternopleuron with 5–7 erect, strong bristles and bristlelike hairs. Abdominal terga 2–4 of male each with a single row of black, hairlike bristles along posterior margin; fifth sternum of male posteriorly with a dense patch of fine hairs, the fourth sparsely bristled (fig. 8); male terminalia as in *dispar* (cf. fig. 4). Length 3.5 mm.

Distribution.—I have seen the following typical *leucogastra*: 2 males, Santiago de las Vegas, Cuba, Feb. 11, 1926; 5 males, same locality, Mar. 31, 1938 (J. Fernandez) [USNM]; 3 males, 2 females, Chilpancingo, Guerrero, Mexico, 3700 ft., Aug. 7, 1954 (J. G. Chillcott; 1 male, Lagos de Moreno, Jalisco, Mexico, 6400 ft., Aug. 19, 1954 (Chillcott); 1 male, 34 mi. S. of Cuernavaca, Morelos, Mexico, 2600 ft., Aug. 4, 1954 (Chillcott) [Canad. Dept. Agr.].

Many of the specimens standing in collections as *leucogastra* must be referred elsewhere. For example, of those recorded by Malloch (1913, Proc. U. S. Nat. Mus. 46: 135), the specimen from Victoria, Tex., is *texensis*, that from Rosser, Tex., is *dispar*, and the two from Georgia are *nitidula*.

P. leucogastra and *dispar* are the most whitish species of the group having conspicuously whitish wing and calypteres and brilliant silvery male abdomen. The characteristically velvet black front, reddish anteriorly, is shared only with *pseudodecora*. *P. leucogastra* and *dispar* are easily confused superficially, but can be distinguished in the male sex by the characteristic bristling of

the sterna of the fourth and fifth abdominal segments (cf. figs. 8 and 9). These can almost always be seen in dried specimens, especially that of *leucogastra*, unless the abdomen is badly collapsed. A somewhat variable character, but apparently quite good for both sexes, is the bristling of the sternopleuron. In *leucogastra*, there are a number of erect bristles and bristlelike hairs, apparently typically five but sometimes more. In *dispar*, there are only three, and occasional additional hairs are small and inconspicuous.

11. **Pholeomyia dispar** (Becker), new status
(Figures 4, 9)

Rhynchomilichia leucogastra var. *dispar* Becker, 1907, Ann. Mus. Nat. Hung. 5: 523, 529 (Tifton, Ga.).
Pholeomyia leucogastra var. *dispar:* Melander, 1913, Jour. New York Ent. Soc. 21: 238.

Diagnosis.—As described for *leucogastra* except as follows: Sternopleuron typically with only three strong bristles and bristlelike hairs, an occasional additional hair weak and inconspicuous; fourth and fifth abdominal sterna of male as in fig. 9, the fourth with a conspicuous group of long hairs on each side on posterior half, the fifth with numerous hairs and bristles but not with a dense posterior marginal area of fine hairs as in *leucogastra* (cf. fig. 8); male terminalia as in fig. 4, the forceps slender.

Distribution.—I have before me 14 males of the species, and 4 females which I associate with them: 5 males, 2 females, Tifton, Ga., Oct. 1896 (topotypic); female, Hudson, Fla., July 13, 1930 (P. W. Oman); male, Goliad, Tex., Oct. 29, 1915; male, Rosser, Tex., Aug. 23, 1905 (F. C. Bishopp), published as *leucogastra* by Malloch (1913); female, Virginia Beach, Va., June 23, 1933 (J. M. Aldrich) [all, USNM]; 4 males, Tifton, Ga. (topotypic); 2 males, Ormond, Fla. (C. W. Johnson); male, St. Augustine, Fla., Apr. 12, 1919 [MCZ]. The females had been placed under *indecora*, the males under *leucogastra*.

Becker attempted to distinguish *leucogastra* and variety *dispar* on the relative lengths of the second abdominal tergum compared with the third and fourth combined, but in the series before me this is merely a matter of telescoping of the abdominal segments. However, he did validate the name *dispar*. I have before me a number of males from the type locality, and probably from the same lot, originally from the Hough collection, as the type material in the Bezzi collection. With this material for analysis, I adopt the name *dispar* for the species. It is superficially very close to *leucogastra*, and following Becker, has usually been identified as a variety of it. The best distinguishing features are the fourth and fifth sterna of the males (cf. figs. 8 and 9).

12. **Pholeomyia nitidula,** new species

Large species with two pairs of strong, well-spaced dorsocentrals and short proboscis, mesonotum appearing shining black as viewed from behind, and terga 2–5 almost entirely silvery.

Male.—Predominantly black; abdominal terga 2–5 silvery except for a small mesal black triangle at base of second tergum and the black apical two-fifths to half of the fifth tergum; wing light brown-tinted; calypteres brown.

Front relatively long and narrow, the length 1.6 times the width at vertex; front at vertex obviously narrower than an eye, 0.35 times the head width, narrowing to 0.19 times at the lunule; postverticals cruciate at tips; outer verticals evident, but slender; eye large, anterior facets moderately enlarged, hind margin virtually straight, with a barely perceptible shallow emargination about midway; face pollinose, slightly concave, epistoma not strongly warped forward and not strongly projecting in profile; parafacial reduced to a line; cheek linear; proboscis well developed, but not unusually elongate, the distal section not longer than the head; third antennal segment small; arista microscopically pubescent.

Mesonotum with two pairs of dorsocentral bristles, the anterior large and strong and well removed from the posterior pair, the interval longer than that between the posterior dorsocentral and the prescutellar acrostical; intrapostsutural longer than mesonotal hairs, but still slender and hairlike and not prominent; mesopleuron with four strong bristles in a single row; sternopleuron with three bristles, only the posterior strong.

Abdominal terga 2–4 each with a row of well-spaced, hairlike bristles near posterior margin, the second with a few additional scattered hairs on mesal third; fifth tergum with a number of hairs on the black apical portion; sterna 4 and 5 and the terminalia as in *dispar* (cf. figs. 4, 9).

Wing venation ordinary for the genus; costal excision moderately deep, slightly longer than the fore crossvein.

Length of body and of wing, 3 mm.

Female.—Unknown.

Holotype and one paratype, both males, Georgia, August (Collection Coquillett). Type No. 64304 in the U. S. National Museum.

This species belongs to a group confused with *leucogastra* in past determinations. The specimens were recorded as *leucogastra* by Malloch (1913, Proc. U. S. Nat. Mus. 46: 135). The species is very close to *dispar*, having the same kind of terminalia and fourth and fifth abdominal sterna in the male (cf. figs. 4, 9). The differences are in color characters, except for the presence of additional setae on the mesal third of the second abdominal tergum in *nitidula*, and it is possible that *nitidula* may ultimately be demonstrated to be only a variant of *dispar*.

13. **Pholeomyia dampfi,** new species
(Figure 7)

Near *leucogastra*, with two pairs of dorsocentral bristles and dorsum of abdomen of male predominantly brilliant silvery, but the wing hyaline or light brown-tinted, calypteres brown, and mesonotum bluish-gray or greenish-gray, viewed from behind.

Male.—Predominantly black to black-brown; abdominal terga 2–5 brilliant silvery except for small median basal triangle on second and the distal two-thirds or more of the fifth; mesonotum and scutellum finely brownish pollinose, the former appearing bluish-gray or greenish-gray when viewed from behind; wing faintly brown-tinted, almost hyaline; calypteres brown.

Front relatively broad and short for the genus, its length 1.25–1.30 times its width at vertex, the width at vertex 0.40 times and at lunule 0.27 times the width of head; postverticals cruciate at tips; outer verticals strong, subequal to the postverticals; eye large, the anterior facets only slightly enlarged, hind margin virtually straight, with an almost imperceptible concavity midway; face pollinose, weakly concave, the epistoma not evident in profile; parafacial only a line; cheek very narrow, almost linear; proboscis short, distal section not as long as head; third antennal segment slightly larger than usual in the genus, broader than long; arista microscopically pubescent.

Mesonotum with two pairs of dorsocentral bristles, the anterior pair relatively short, half the length of the posterior, and separated from them by slightly less than the distance from posterior dorsocentral to the nearest acrostical; intrapostsutural bristle, between posterior dorsocentral and acrostical bristles, only weakly developed, little longer than hairs; four strong mesopleural bristles in a single row; three sternopleural bristles, the posterior longest and strongest.

Dorsum of abdominal terga 2 through 4 typically with only a single row of well-spaced hairlike bristles near posterior margin; fifth tergum with numerous hairs on posterior two-thirds or more, chiefly on the dark part of the tergum and ending at the submarginal row of long bristles; abdominal sterna 4 and 5 as in fig. 7, sparsely beset with bristles and hairs, the laterals on 5 well developed; male terminalia as in *leucozona* (cf. fig. 3).

Wing venation ordinary for the genus; costal excision short.

Female.—As described for male, except for the terminalia and abdominal sterna, and as follows: Abdomen entirely brown to black, the entire dorsum beset with hairs; front broad, slightly broader than long and wider than an eye, at the vertex slightly over and at lunule slightly under two-fifths the width of head, the sides appearing virtually parallel; face correspondingly broad; eye facets uniform in size; third antennal segment larger than usual in the genus, nearly twice as broad as apical diameter of second segment.

Length of body and of wing, 2.5 mm.

Holotype male, allotype, and 20 paratypes (10 males, 10 females), Caves of Jobitzinal, near Flores, Petén, Guatemala, Nov. 29, 1925, captured in cave (A. Dampf); 1 male paratype, Teapa, Tabasco, Mexico, July 27, 1954, in cave (Ryckman, Christianson, Fisher). In the U. S. National Museum, Type No. 64305.

Dr. Aldrich noted in his card catalogue (U. S. Nat. Mus.) that Dampf wrote in December 1926 "that he had reared a lot more from bat dung, and says they follow the bats into the caves several hundred meters." No material of this rearing is available for verification, although the circumstances suggest that the same species was probably involved.

Three other males from the same lot as the type, and a male from Guatemala City, Guatemala, 5000 ft., March 1932 (C. N. Ainslie) [USNM] differ in having the central two-thirds of the second tergum extensively haired, rather than the single row. I can find no other differences, and conclude that this is only an occasional variant from the typical form. One male shows an intermediate condition, with more and finer bristles in the marginal row, and a few scattered hairs on the disk of the tergum.

This species is close to *leucogastra*, and stood in the collection under that name. It is likewise close to *dispar* and *nitidula*, and the four form a small complex of some difficulty. However, the fourth and fifth sterna of the males are of three quite different kinds (cf. figs. 7–9).

14. **Pholeomyia robertsoni** (Coquillett)

Milichia robertsoni Coquillett, 1902, Jour. New York Ent. Soc. 10: 187 (Inverness, Fla.).
Rhynchomilichia robertsoni: Becker, 1907, Ann. Mus. Nat. Hung. 5: 526.
Pholeomyia robertsoni: Melander, 1913, Jour. New York Ent. Soc. 21: 238.

Diagnosis (male).—Thorax brown-gray plolinose; abdomen with terga 2–4 silvery on sides and anterolaterally, the second and third each brownish-gray dorsally in a broad triangular area with base along posterior margin, the fourth likewise but its silvery pollen forming a continuous anterior marginal band; fifth tergum predominantly silvery, brown-black on distal fourth to third, beyond the row of bristles; wing and calypteres whitish.

Postvertical bristles cruciate; outer verticals well developed for a male; face gray pollinose, moderately concave; cheek linear; proboscis not elongate, distal section shorter than head. Mesonotum with two pairs of strong dorsocentral bristles; mesopleuron with four strong bristles in a single row. Second to fourth abdominal terga with a few hairs, in about one irregular row, in addition to the posterior marginal row of hairlike

bristles. Wing with costal excision small. Length of wing, and probably of the body (collapsed in type), 2 mm.

The holotype [USNM] and only specimen known to me is collapsed, but fortunately the above diagnostic characters can be seen. It has not been dissected, so that the pattern of the dorsum of the abdomen will not be spoiled unless and until absolutely necessary. The abdomen is too curled for proper examination of the fourth and fifth sterna, but it appears that they may resemble those of *dispar* (cf. fig. 9), although the side hairs are not as densely placed.

One male, Elfers, Fla., Apr. 14, 1952 (J. R. Vockeroth) [Canad. Dept. Agr.] may be *robertsoni*, but the brown areas on terga 2 through 4 are much reduced, those on 3 and 4 to narrow median areas along posterior margins of each tergum. It is possible that this represents variation in *robertsoni*.

15. **Pholeomyia texensis,** new species

(Figure 10)

Small species near *leucogastra*, with two pairs of dorsocentrals and short proboscis, but abdominal terga 2–4 with two to several rows of hairs or hairlike bristles, those terga chiefly silvery but at least tergum 2 broadly brown on mesal third or more.

Male.—Predominantly black to brown-black; abdominal terga 2 through 5 predominantly silvery, the second always broadly brown on mesal third or more, the third and fourth typically entirely silvery but occasionally with some brown mesally along posterior margin, the fifth black on extreme sides and sometimes at apex mesally; mesonotum and scutellum grayish or light brownish-gray pollinose, the former appearing bluish-gray or greenish-gray when viewed from behind; wing and calypteres apparently light brownish, but color possibly affected by the poor condition of preservation.

Front relatively short and broad, its length only 1.17 times its width at vertex, the front at vertex 0.44 times the head width, narrowing to 0.26 times at the lunule; postverticals cruciate at tips; outer verticals well developed; eye large, anterior facets moderately enlarged, hind margin of eye distinctly though shallowly emarginate about midway; face pollinose, weakly concave, epistoma not strongly warped forward, and not evident in profile; parafacial reduced to a line; cheek narrow but wider than usual, over half the breadth of a palp; proboscis short, distal section not as long as head; third antennal segment small; arista microscopically pubescent.

Mesonotum with two pairs of dorsocentral bristles, the anterior pair moderately well developed; intrapostsuturals not developed; four strong mesopleural bristles in a single row; three sternopleural bristles, the posterior strong.

Dorsum of abdomen sparsely covered with coarse hairs, the second tergum with two to three rows, the third and fourth each with one row of coarse hairs, the rows more or less irregular, in addition to the posterior submarginal row of hairlike bristles on each tergum; fifth tergum more extensively haired, only a basal band bare; sterna four and five (fig. 10) with unique pattern of dense sublateral areas of fine hairs flanking a median bare stripe; terminalia as in *dispar* (cf. fig. 4).

Wing venation ordinary for the genus; costal excision of moderate depth, about twice the length of fore crossvein.

Female.—As described for male, except for terminalia and sterna, and as follows: Abdomen entirely brown to black-brown, the dorsum with numerous coarse hairs; front nearly square, as broad as long and approximately half the width of head; face correspondingly broad; eye facets of uniform size; cheek slightly broader than in male, but still narrow; interfrontal hairs quite distinct, and often appearing set on incomplete, linear, interfrontal plates.

Length of body and of wing, 2–2.25 mm.

Holotype male, allotype, and 15 paratypes (9 males, 6 females), San Antonio, Tex., Jan. 30, 1935 (E. V. Walter), "nest of cut ant"; male paratype, Victoria, Tex., Apr. 1, 1907 (J. D. Mitchell). In the U. S. National Museum, Type No. 64306. Seven other specimens (4 males, 3 females) of the San Antonio series are in poor condition and are not included in the type series. The circumstances of the rearing of this series are noted in the introduction under the heading of "Biology." The Victoria specimen was recorded as *leucogastra* by Malloch (1913, Proc. U. S. Nat. Mus. 46: 135).

The unique pattern of hairs of bristles on the fourth and fifth sterna of the male is the surest distinguishing feature of this species.

16. **Pholeomyia leucozona** Bilimek

(Figure 3)

Pholeomyia leucozona Bilimek, 1867, Verh. zool.-bot. Gesell. Wien 17, Abh.: 903 (Mexico).

Pholeomyia cacahuamilpensis Herrera, 1892, El Estudio: Organo Inst. Med. Nac. Mexico 4(8): 272. NEW SYNONYM (Unnecessary renaming of *leucozona*, on ground that cave species should have more appropriate names, this species being taken in the cave Cacahuamilpa).

Pholeomyia leucozona: Hendel, 1911, Wien. Ent. Ztg. 30: 40, figs. 5–7 (redescription, from type series).

Species with two pairs of dorsocentral bristles and short proboscis, the male with characteristically patterned abdomen.

Male.—Predominantly black; mesonotum and scutellum, viewed from behind, brown to brownish gray-pollinose; abdominal pattern near that of *Pholeomyia praesecta* Becker from Peru (Becker, 1907, Ann. Mus. Nat. Hung. 5: pl. 12, fig. 4) but the dark central area on tergum 2 nearly quadrate, almost covering the dorsal aspect of that tergum,

the sides silvery; terga 3 and 4 silvery, tergum 5 silvery at base but black on most of its surface; wing light brown; calypteres brown.

Head as figured by Hendel; front at vertex wider than an eye and 0.42 times the width of head, strongly narrowing towards the antennae; postverticals cruciate at tips; outer verticals strong; lunule only narrowly visible; hind margin of eye virtually straight; facets on anterior part of eye only slightly enlarged; face dull, pollinose; epistoma not strongly warped forward and not projecting in profile; cheek linear; proboscis short, distal section less than length of head; third antennal segment of moderate size; arista microscopically pubescent.

Mesonotum with two pairs of dorsocentral bristles, the anterior strong but only half the length of posterior; mesopleuron with four strong bristles in a single row; three sternopleural bristles, the posterior strong.

Dorsum of abdomen with numerous coarse hairs, the second with five to six irregular rows, the third and fourth each with a single row along posterior margin, and the fifth with numerous hairs over its surface except on the silvery band at base; sterna 4 and 5 as in ***dampfi*** (cf. fig. 7); terminalia as in fig. 3, the forceps slightly broader than in ***dispar***, ***leucogastra***, etc. (cf. fig. 4).

Wing damaged, but apparently ordinary for the genus, as figured by Hendel; costal excision relatively small, not as conspicuous as in Hendel's figure.

Female.—As described for male, except for terminalia, sterna, and as follows: Abdomen entirely brown to brown-black, the dorsum with numerous coarse hairs; front slightly broader than in male, at the vertex wider than an eye and 0.44 times the width of head, narrowing slightly towards the antennae but not as strongly as in male, the face obviously wider; eye facets of uniform size, all small; cheek linear, only insignificantly wider than in male.

Length of body, 2.5 mm.

I have before me two males and two females of Bilimek material from Mexico [Naturhist. Mus., Wien]. The specimens are no longer in good condition, but they have made it possible to see a number of the essential points, as described above. One male, which bears the handwritten labels "14. Jaenner," "Bilimek/Cacahua/milpa," and "Pholeomyia leucozona" in an old script, is apparently one of the original series, and I have labeled it as Lectotype. Two specimens, a male and a female, bear a printed label "Bilimek/Mexico/1871," the female with "Type" written on the label. The date of collection is subsequent to the original publication and although these specimens are apparently conspecific with the Lectotype, they cannot be considered as part of the original syntype series. The second female is labelled only "Mexico." In order to preserve the appearance of the Lectotype, already in none too good condition, the 1871 male was dissected for study of the sterna and terminalia (fig. 3).

This species, the type-species of the genus, is distinguished from its congeners as noted in the key.

ADDENDUM

Pholeomyia comans, new species

Small species near ***texensis***, but the abdomen chiefly brown, and terga 2–5 with numerous hairs.

Male.—Predominantly brown to black; abdomen predominantly brown in dorsal aspect, with some silvery pollen on posterolateral corner of second tergum, on narrow bases of terga 3 and 4, broadening laterally, and narrowly on base of fifth tergum, especially sublaterally; mesonotum and scutellum as in ***texensis;*** wing apparently whitish, but possibly affected by mounting from fluid; calypteres whitish, light brown margined.

Structural details as in ***texensis***, except as follows: Front very slightly wider; dorsum of abdomen densely covered with hairs, with approximately four irregular rows on terga 3 and 4 in addition to the posterior marginal row of bristles, the hairs finer and more closely set than in ***texensis***; sterna 4 and 5 similar to ***texensis*** (cf. fig. 10), but the dense patches of hairs are larger and nearly coalesce mesally; male terminalia as in ***dispar*** (cf. fig. 4).

Female.—As described for ***texensis***.

Length of body and of wing, 1.75—2 mm.

Holotype male, allotype, and 80 paratypes (40 males, 40 females), Flatwoods, Rapides Parish, Louisiana, emerged Feb. 18–28, 1959; reared from one-day old detritus taken immediately from fungus gardens at depth of 6 feet in nest of ***Atta texana*** (John C. Moser, U. S. Dept. of Agriculture, Southern Forest Experiment Station). In the U. S. National Museum, Type No. 64688.

The species is very close to ***texensis***, but is easily distinguished by the predominantly brown, densely haired abdomen of the male. The male keys to couplet 15, and may be separated from the last three species in the key by the combination of brown color and dense hairs just described. The female runs directly to ***texensis*** in couplet 20, and I am unable to distinguish the two species in this sex. Perhaps it will be possible when females of ***texensis*** in better condition are available.

According to information kindly furnished by Mr. Moser, this is "the primary insect which breaks down the recent detritus in the detritus cavities. It is very abundant in all nests, and adults often fly out when the cavities are opened." Approximately 200 adults were reared, but a number are teneral and have not been included in the type series.

Pholeomyia obscura, new species

Small species near ***texensis***, but the male abdomen entirely dark.

Male.—Black to brown-black, only the calypteres whitish, and the wing slightly so; mesonotum, when viewed from behind, only slightly bluish- or greenish-gray and then obscurely so.

Structural details as described for *texensis*, except as follows: Front more strongly narrowed anteriorly; interfrontal hairs, except the foremost in each row, fine, short, and inconspicuous against the velvety black front; second to fourth abdominal terga each with 1–2 irregular rows of hairs in addition to the posterior marginal row of bristles, the hairs finer and slightly more closely set than in *texensis*; sterna 4 and 5 approximately as in *dampfi* (cf. fig. 7); terminalia as in *dispar* (cf. fig. 4).

Female.—Unknown (see comment).

Length of body and of wing, 1.25–1.5 mm.

Holotype male, Austin, Texas, Nov. 9, 1958. In the U. S. National Museum, Type No. 64689. Paratypes, 40 males, Austin, Texas, Oct. 5, 10, 18, Nov. 9, 13, 1958, on flowers of *Parthenium hysterophorus* L. (Lynn Throckmorton).

A series of females was taken at the same time and place, but unfortunately males of *texensis* were also present, and I see no differences in the females. Very probably, females of *obscura* will run to *texensis* in the key, as do those of *comans*.

The males of *obscura* key only to couplet 9, and will be separated from all other males in the group that follows by the entirely black abdomen. The relatively plain bristle and hair pattern of sterna 4 and 5, as well as the entirely black abdomen, will separate *obscura* from *texensis* and *comans*, two closely related species in the same region. *P. obscura* most closely resembles *politifacies*, and could easily be mistaken for it except for the dull pollinose face of *obscura*.

MYCOPHILA FUNGICOLA FELT: A REDESCRIPTION AND REVIEW OF ITS BIOLOGY (DIPTERA, ITONIDIDAE)[1]

RICHARD H. FOOTE[2] AND CHARLES A. THOMAS[3]

ABSTRACT

Mycophila fungicola Felt has been recorded from California and the central and eastern United States. It is becoming an increasingly important pest of mushrooms in southeast Pennsylvania. The adult, pupa, and larva are redescribed and figured, and outstanding features of paedogenesis are outlined. This paper discusses the type of damage occasioned by the larvae, and records some important features of the biology of this species.

Mycophila fungicola was described from San Rafael, California, by Felt (1911), who was perhaps the first to note it as a pest of cultivated mushrooms in the United States. For a number of years the larva of this mushroom midge has been recorded in Virginia, southeastern Pennsylvania, Ohio, and Indiana as a minor pest. However, as long ago as 1942, Thomas stated that this fly appeared to be gaining in importance, and during the last 3 years a further increase in its abundance has occasioned considerable concern to growers in the Kennett Square area of Pennsylvania.

This paper is presented in response to increased requests for information about the morphology and biology of this potentially important fly. A redescription and detailed illustrations of the adult, larva, and pupal exuvium supplement the morphological information presented for *fungicola* by Felt (1911, 1913) and Pritchard (1947, 1953), and a further discussion summarizes the available information on its biology.

[1]Journal Series No. 2298, Pennsylvania Experiment Station. Accepted for publication November 7, 1958.

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Mycophila fungicola Felt

Mycophila fungicola Felt, 1911, Jour. New York Ent. Soc. 19: 33 (n. gen., n. sp.; descr. ♂); Felt, 1913, New York State Mus. Bull. 165: 161; figs. 38–40 (descr. larva, ♀; figs. male antenna, wing); Edwards, 1938, Proc. Roy. Ent. Soc. London (B), 7: 253 (comp. with *M. barnesi* n. sp. and *M. speyeri* Barnes; figs. for these two spp.); Pritchard, 1947, Ent. Americana (n.s.) 27: 64, 65 (redescr. of gen. and sp.; ♂ lectotype designated); Nayar, 1949, Proc. Roy. Ent. Soc. London (B), 18: 81; fig. 5–7 (in key to world species of *Mycophila*); Pritchard, 1953, Bull. California Ins. Surv. 2(2): 132 (key to *M. fungicola* and *M. barnesi*; both occur in California).

MALE.—*Head.*—Subspherical, eyes occupying most of head surface and dorsally united by a bridge not exceeding two facets in width. Antennal flagellum with nine full segments, or if with eight, the terminal segment constricted medially; distal margin of area of minute spines of segments 1 through 3 each with a short transparent appendage; proximal flagellar segment unlike those following in being narrowed prox-

imally and with heavy bristles in a diagonal row; third flagellar segment (fig. 7) with proportions of proximal enlargement to distal narrowed portion about 3:2; a transverse row of long bristles and several shorter bristles scattered over remainder of surface of enlarged portion. Palpus (fig. 6) two-segmented, the second segment acute and arising subapically from the first.

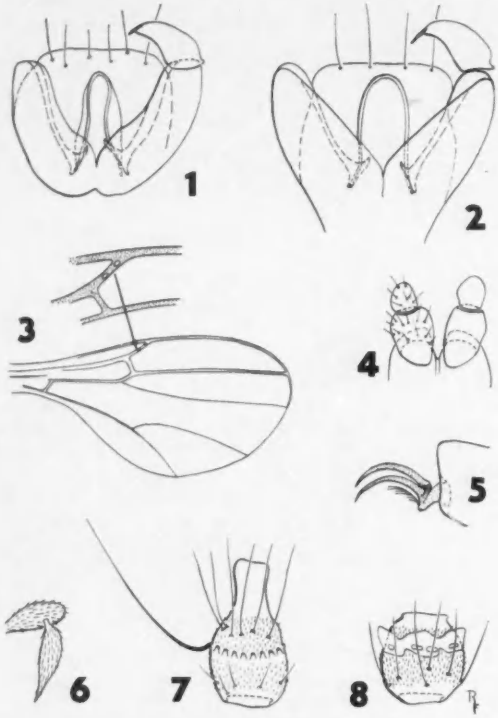

FIG. 1.—Remounted terminalia, lectotype ♂, San Rafael, Calif. FIG. 2.—Male terminalia from specimen collected at Kennett Square, Pennsylvania. FIG. 3.—Right wing of ♂, dorsal view, with detail showing sensory pores. FIG. 4.—Terminal lobes of ♀ abdomen, ventral view. FIG. 5.—Claws of hind leg, ♂. FIG. 6.—Right palpus, ♂. FIG. 7.—Third antennal segment, ♂. Only one of the longest hairs is shown. FIG. 8.—Third antennal segment, ♀.

Wing (fig.) 3.—Proportions of length to width about 15: 8, branches of radius much stouter than other veins; R_1 about 1.2 times as long as R_s, with one or two sensory pores, the anterior-most always present; veins C, R_5, M_{1+2}, Cu_1, and A about equidistant along a transverse line drawn halfway between base and tip of wing; vein Cu_1 branching from vein A at a point directly posterior to the union of R_s with R_5; veins R_5 and M_{1+2} parallel along their distal two-thirds.

Legs.—Proportions of hind femur, tibia, and tarsomeres, respectively: 24:20:10:4:3:2:4, the fifth tarsomere distinctly twice as long as the preceding one; tarsomeres covered with very slender hairs not resembling scales. Claws on all legs simple, evenly curved, about as long as width of fifth tarsomere; empodium approximately one-half the length of a claw, with some fine, fringing hairs.

Terminalia (figs. 1 and 2).—Dististyle about 0.5 times as long as basistyle, tapering from a heavy base, with an apical spine about 0.2 times as long as dististyle. Basistyle about 2.5 times as long as wide, joined with opposite basistyle medially; with a lightly sclerotized internal rod rising from the distal end and lying along the inner margin, expanded medially to engage the proximal ends of the arms of tegmen. Tegmen of various shapes according to method of mounting, but rather broadly rounded apically, its arms slender throughout.

FEMALE.—*Head* (except antenna), wing, and legs as in male. Antennal flagellum with eight full segments, or if with seven, the terminal segment constricted medially; no short transparent appendage present on any of the segments; but each segment with two to four platelike "sensorial processes" which together completely surround the segment, each process arising from several "pores" or from a single long, narrow pore and having a lobed or digitate distal margin. Flagellar segment 3 (fig. 8) subspherical with almost no indication of a distal narrowed portion; a number of fine hairs scattered over proximal half of segment. Ovipositor lobes (fig. 4) paired, each pair consisting of two ovate segments, the proximal segment 2.0 to 2.2 times as long as distal; paired lobes together extending well caudad of tenth tergite; spermatheca single, ovate, well sclerotized.

PUPAL EXUVIUM (fig. 9).—Antennal case free of body and about 0.25 times as long as total length of body, with no clear divisions corresponding to antennal segments; pupal horns very long and slender. Remainder of exuvium in too poor condition to describe.

LARVA (figs. 10–14).—Sclerotized portion of head 1.5 times as long as greatest width, usually partially or entirely withdrawn inside the first segment; antenna with one segment, about 5 times as long as greatest width, acuminate, mounted on a prominent elevation of head wall; internal structure as shown in fig. 10. Position of spatula, when present, as shown in fig. 10; spatula with three broad, well-separated, anteriorly directed teeth and a caudally directed triangular-shaped piece, very dark to completely transparent, as shown in figs. 13 and 14; in some specimens only a bare suggestion of anterior teeth (fig. 14); in some the spatula entirely absent. In most specimens a dark, granular, boat-hook-shaped structure (fig. 12), the arms of which are often separated from each other, situated just under dorsal surface of second segment directly opposite the position normally occupied by ventral spatula but most fully developed in specimens

that lack spatula, presenting the appearance at low magnification of a spatula of different shape. Caudal structure as shown in fig. 11

MATERIAL EXAMINED.—Male lectotype (designated and so-marked by A. E. Pritchard): San Rafael, Calif., 7 Sept. 1897, reared from mushroom; in collection of the U. S. National Museum. About 500 ♂♂, 500 ♀♀, 300 larvae, 20 puparial exuvia; Kennett Square, Pa., 1 Aug. 1957, C. A. Thomas; reared from a variety of *Agaricus campestris*, the commercial mushroom; all in collection of the U. S. National Museum.

MORPHOLOGY

Among its relatives the genus *Mycophila* is distinctive in possessing a transparent process on each of the first three male flagellar segments and "sensorial processes" on all but the terminal female flagellar segment. The male processes exhibit various shapes (shown in fig. 7) largely according to the amount of shrinkage they undergo during the slide-mounting process. Although variation in the number and position of sensorial processes in the female cannot be accounted for in this way, the shape of their distal margins may well be a victim of shrinking, for they appear to be transparent and very delicate. Examination of a series of slide-mounted males and females from Kennett Square indicates the extreme variation in these structures and their lack of value as taxonomic characters for the separation of species within the genus.

In every reference to the type of *fungicola* the male terminalia are reported to be mounted laterally; therefore, their characters could not be ascertained. We have dissected the terminalia from the male lectotype and remounted them for observation, and a drawing is presented in fig. 1. The somewhat collapsed appearance in comparison with that of a recently mounted male from Kennett Square (fig. 2) is characteristic of specimens that have been in balsam for long periods of time, and is also indicative of the variation encountered in the soft parts of balsam-mounted specimens.

These insects have a remarkable life cycle. Although they can develop like other fly species from the egg through the larval and pupal stages to the adult, the larvae of *fungicola* can also produce living young within themselves, a phenomenon called paedogenesis. An extensive discussion of this mode of reproduction has been presented by Seguy (1950). The junior author has seen as many as 31 "daughter larvae" emerging from the body of a "mother larva."

Two distinct forms of larvae are identifiable in mushroom cultures. The paedogenic form, which gives rise to living larvae, apparently lacks any true form of ventral spatula, but in living larvae a granular structure just under the dorsal surface of the second segment is very evident and may be easily mistaken for it. The function of this granular structure is not known. The other form of larva metamorphoses into a pupa, and most mature specimens possess a spatula in addition to the structure mentioned above. The spatula is distinctly tridentate and varies from completely transparent to completely opaque. One showing intermediate pigmentation is shown in fig. 13. The spatula is apparently never formed until the larva has almost completed the development of its final instar.

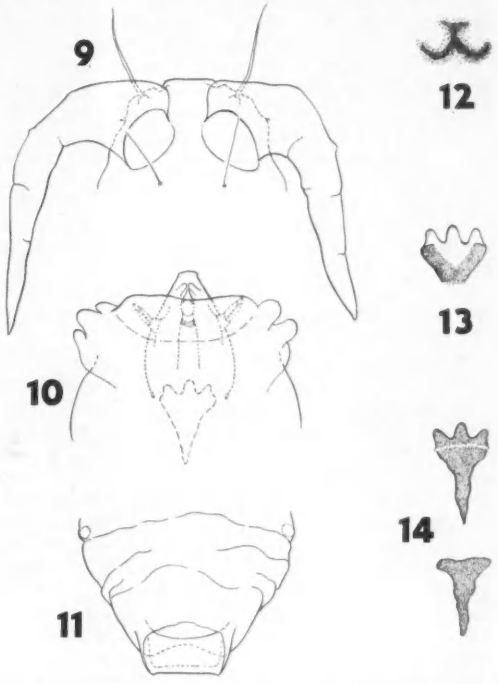

FIG. 9.—Antennal sheaths and pupal horns of pupal exuvium. FIG. 10.—Ventral view of anterior end of full-grown larva. FIG. 11.—Ventral view of caudal end, same. FIG. 12.—Dorsal granular structure of paedogenic larva. FIGS. 13 and 14.—Variations in form and opacity of spatula.

BIOLOGY

In reference to these larvae as pests, Thomas (1931) states that they "may appear in large numbers on the caps or under the gills of mushrooms or crawling upon the casing soil. Although abundant, little or no injury may result. At times, however, small holes similar to those caused by phorid fly larvae may be chewed in the tissue. They may also occasionally feed upon the mycelium in the beds."

Davis (1938) stated that adults of *Mycophila fungicola*, common at the Arlington Experiment Farm, Virginia, are ". . . very inconspicuous, as they remain flat against the bed boards and usually fly only when disturbed. The larvae are bright yellow or orange, one-fourth inch or less in length. At times these may appear in large

numbers upon the casing soil and mushrooms, and if sufficiently numerous may cause injury to the spawn and to the mushrooms by eating small holes into the stems and caps. Normally, however, these flies are minor pests of mushrooms."

The larvae feed on mushroom mycelium and on molds in the compost in the beds. They move up into the casing soil, feeding on the mycelial strands and on the tissues at the base of the mushroom stem; they then burrow just under the mushroom "skin" and up into the veil and gills, making these parts slimy, streaked, and shredded. Bacteria carried about by the larvae cause the mushroom stem surface to be covered with a yellowish-white slime. The gills are slowly destroyed and slimy yellowish bacterial colonies grow on the broken-down tissues. The larvae may be abundant at the top of the stem next to the gills.

Canneries refuse to accept such mushrooms, as some of the larvae float out with the broth when the mushrooms are cooked, and many may still remain among the gills after canning. The larvae do not burrow up through the interior of the mushroom stem and cap in the manner of the sciarid and phorid larvae.

When *fungicola* larvae have fed on the mycelium in the compost, spots bare of mushrooms may appear in these feeding areas. Since the larvae usually develop in the compost in the bed, and since the tiny orange-and-black flies appear only occasionally, immense numbers of these larvae may accumulate in the beds before a grower becomes aware of their presence. When infested beds are watered, thousands of larvae may come up onto the soil surface, where they either crawl around on the moist soil or up onto the mushrooms, or pile up in tangled squirming masses, sometimes even on the bed boards, and fall off onto the walks. Whenever larvae crawl along dry surfaces, they coil and jump by contraction of their body muscles, and continued exposure to excessive desiccation causes them to shrivel and die. They can withstand total submergence in water for several days, however. These larvae are positively phototropic, hence may be most numerous on bed surfaces where there is some light, such as near windows, fly-trap lights, or along the edge of the bed next to the center aisle where light from the ventilator may show. In culture bottles they congregate mostly on the side toward lights, moving around to the light side when the bottle is rotated.

These tiny larvae have been found feeding on molds growing in moist protected places in old corn leaves, husks, and cobs lying in cornfields. Therefore, they may appear in mushroom houses near such areas. However, this is probably not their only source of food, and they may feed on molds growing on old organic debris in nearby woodlands or on piles of discarded mushrooms, stem stumps, and other material from the beds.

Use of casing soil from an old cornfield might transfer *fungicola* to mushroom houses unless this soil is treated with steam or a soil fumigant. Larvae have also occasionally survived the compost pasteurization in the beds by being in wet lumps that did not attain a high enough temperature, or in cracks and holes in the boards.

The larvae may sometimes be found feeding in the compost soon after the spawn is planted and several weeks before any casing soil is placed on the beds.

Mushroom injury by itonidid larvae has been studied in England by Hussey and Wyatt (1958) who summarized the answers to a questionnaire sent to 82 growers. They conclude that "45 percent of the growers who attained pasteurizing temperatures of less than 130° F. at peak heat experienced cecid [itonidid] damage (18 percent seriously), while 68 percent of those reaching 131° F. and above had attacks (32 percent seriously)," and suggest that the greater incidence under theoretically more hygienic conditions may be due to the elimination of some natural control factor, such as predatory nematodes or diseases of the larvae.

The junior author has occasionally found nematodes in large numbers in spawn cultures containing larvae. The larval population eventually declines, with the nematodes clustering about and apparently feeding on those that are dead and dying. As Hussey and Wyatt also state, nematodes occur in the bed compost where laruae are common, but their relationship to the larvae is unknown.

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A REDESCRIPTION OF THE MALE OF SITEROPTES RENIFORMIS KRANTZ 1957 WITH NOTES ON THE FAMILY PYEMOTIDAE (ACARINA)[1]

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ABSTRACT

The male of *Siteroptes reniformis* is redescribed from type material. Key generic characters used by earlier authors for the Pyemotidae are discussed and revised, and a key is given to all genera of the family except *Phthiroides*.

The following description is based on a re-examination of type material at the U. S. National Museum, Washington, D. C.

Siteroptes reniformis Krantz

Male (Fig. 1).—Morphologically distinct from female. Total body length, including the gnathosoma, averages 160 μ. Width of idiosoma between the insertions of coxae II and III averages 87 μ. Gnathosoma reduced and bearing two pairs of short papilliform organs. Propodosoma partly covered by a triangular plate on which are inserted four pairs of setae; setae II somewhat shorter than setae I; setae III twice the length setae II; setae IV whiplike, approximately four times the length of setae III. Hysterosoma with a broad dorsal plate on which three pairs of setae are inserted, the most lateral pair of which is long and whiplike. With a pair of short setae posterior to the hysterosomal plate and anterior to a small pebbled terminal plate. Terminal plate with a pair of clubbed setae situated on lateral protuberances, each of which is flanked posteriorly by a minute spine. Legs short, stout; tarsi II and III with caruncle and claws; tarsus I with an empodial claw and two prominent sensory clubs; tarsus IV with caruncle and broad, well-developed claw; tibia IV with dorsal sensory club and adjacent seta on a single insertion.

The female of *S. reniformis* has been described elsewhere (Krantz 1957).

Jacot (1936) separated the genus *Pyemotes* Amerling 1862 (= *Pediculoides* Targioni-Tozzetti 1878) from other pyemotids on the basis of the pointed posterior aspect of the idiosoma. Krantz (1957) added the character of the shape of the gnathosoma which, because of its closely appressed palps and hypognathous aspect, appears circular in outline (fig. 2). It has since been found that various members of the family besides those falling within the genus *Pyemotes* may have the abdomen bluntly pointed and that, as a result of mounting techniques, the gnathosoma of mites other than those belonging to this genus may appear circular. In addition, mites of the genus *Pyemotes* have recently been seen which do not show a circular gnathosomal shape (fig. 9). The character of closely appressed palps, however, seems to be a reliable definitive character for the genus. There are indications that gravid females of the genus *Pyemotes* may be separated from gravid females of *Siteroptes* by the extent of opisthosomal swelling. The idiosomal dilation of

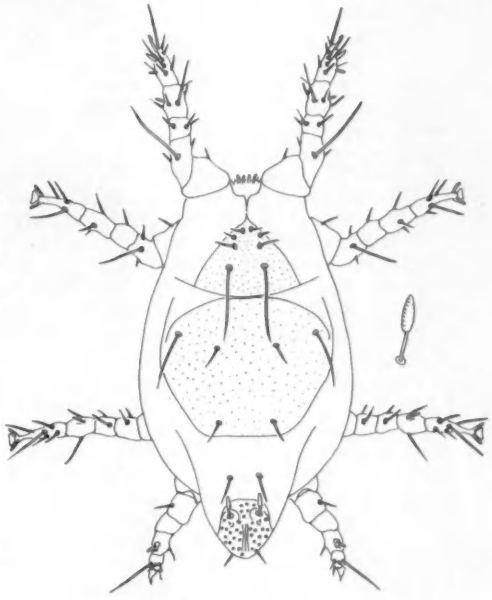

FIG. 1.—*Siteroptes reniformis* Krantz, dorsal aspect of male.

Pyemotes ventricosus (Newport) (fig. 2) extends anteriorly only to legs IV, while the swelling of gravid *Siteroptes graminum* (Reuter) (fig. 4) includes not only the opisthosoma but the metapodosoma as well.

The genus *Pygmephorus* Kramer 1877 was characterized by Jacot (1936) as having one or two pairs of propodosomal setae and a swollen tarsus I. Jacot further stated that tarsus I of *Pygmephorus* is much longer than tibia I. An examination of several specimens of *Pygmephorus*

[1]Accepted for publication October 21, 1958.

has shown that the discrepancy in segmental lengths may be quite small. It appears also that tarsus I is, in reality, the fused tibia and tarsus, and that the tibia as conceived by Jacot actually is genu I (fig. 8). The width of the tibiotarsus is either equal to or slightly greater than that of genu I.

The genus *Resinacarus* Vitzthum 1927 differs from *Pygmephorus* in that the former possesses three pairs of propodosomal setae while *Pygmephorus* has one or two pairs. While leg I of *Resinacarus resinatus*, the type species, is nearly equally expanded along its entire length, the member is considerably heavier than legs II–IV. Apparently tibia and tarsus I are fused as in *Pygmephorus*. Undescribed pyemotids with the propodosomal characters of *Resinacarus* have been found to have a greatly swollen tibiotarsus I which may be up to twice the width of the genu and over twice its length (fig. 7). The tibiotarsal claw in these forms is heavy and pincerlike, the structure of which enables them to grasp the hairs of small rodents on which they commonly are found. One species taken from cells of bees of the genus *Nomia* possesses the typical heavy claw, but tibia and tarsus I are not fused, nor is there the usual expansion of these segments (fig. 6).

Lombardini (1949) described the genus *Pavania* as having hooklike rather than stylettiform chelicerae. The genus *Dolichocybe* Krantz 1957, subsequent to the original description, was found to have similar cheliceral structures (fig. 5). These genera may be separated by differences in gnathosomal shape, as well as by the difference in the numbers of propodosomal setae.

In addition to the genera mentioned above, Baker and Wharton (1952) list *Acarophenax* Newstead and Duvall 1918, *Phthiroides* Oudemans 1937, and *Tarsonemoides* Trägårdh 1904 in the family Pyemotidae. *Acarophenax* may be separated from other pyemotids by its lack of claws on tarsi II–IV. The figure of *Tarsonemoides* in the original generic description indicated that *T. termitophilus*, the type species, was a tarsonemid rather than a pyemotid. Sellnick (1958) includes the genus in the Tarsonemidae in his review of mites found associated with agriculture in North Sweden. The author has seen neither specimens nor figures of *Phthiroides*.

The following key to females has been constructed in light of the foregoing discussion. The genus *Phthiroides* is not included.

1. Without claws on tarsi II–IV ..... **Acarophenax** Newstead and Duvall 1918
   With claws on all legs 2
2. Tarsus I with two claws; chelicerae hooklike 3
   Tarsus I with only an empodial claw; chelicerae not hooklike 4
3. Propodosoma with two pairs of setae; gnathosoma as broad, or broader than, long ..... **Pavania** Lombardini 1949
   Propodosoma with three pairs of setae; gnathosoma narrow and elongate (Fig. 3) ..... **Dolichocybe** Krantz 1957
4. Tarsus I subequal to or shorter than tibia I; claw of tarsus I never heavy and pincerlike; dorsum of propodosoma always with three pairs of setae 5
   Tibia and tarsus I usually fused, the resulting segment always longer than genu I, or if not fused, with heavy pincerlike claw on tarus I; propodosoma with one to three pairs of setae 6
5. Palpi closely appressed to gnathosoma, the latter usually appearing circular in outline; posterior end ot idiosoma usually bluntly pointed ..... **Pyemotes** Amerling 1862
   Palpi free distally from gnathosoma, the latter appearing elliptical in outline; idiosoma usually truncate or angled behind ..... **Siteroptes** Amerling 1861
6. Propodosoma with three pairs of setae; when present, tibiotarsus I swollen, as much as twice the width of genu I ..... **Resinacarus** Oudemans 1937
   Propodosoma with one or two pairs of setae; tibiotarsus I with little or no apparent swelling, never attaining twice the width of genu I ..... **Pygmephorus** Kramer 1877

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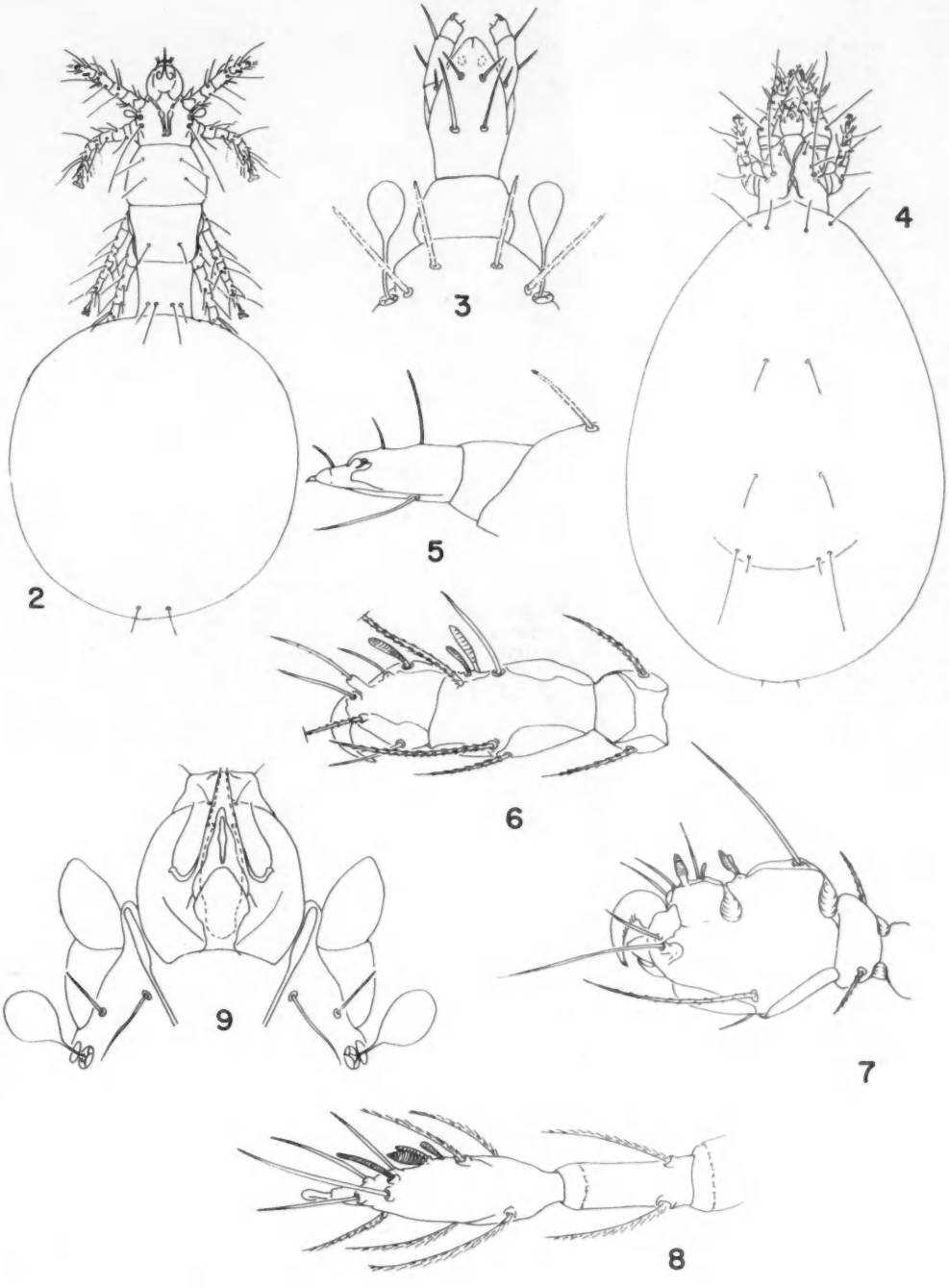
EXPLANATION OF FIGURES

FIG. 2.—*Pyemotes ventricosus* (Newport), gravid female (after Baker et al. 1956, "Manual of Parasitic Mites," with permission of National Pest Control Association, Elizabeth, N. J.). FIG. 3.—*Dolichocybe keiferi* Krantz, dorsal aspect of gnathosoma and portion of propodosoma. FIG. 4.—*Siteroptes graminum* (Reuter), gravid female (after Baker and Wharton 1952, with permission of The Macmillan Company, New York, N. Y.). FIG. 5.—*D. keiferi*, lateral aspect of gnathosoma with one palpus removed to show the hooklike chelicerae. FIG. 6.—Leg I of *Resinarcus* sp. without fusion of tibia and tarsus. FIG. 7.—Leg I of *Resinarcus* sp. with fused tibia and tarsus. FIG. 8.—Leg I of *Pygmephorus* sp. FIG. 9.—*Pyemotes* sp., dorsal aspect of gnathosoma and portion of propodosoma.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OBITUARIES

James George Needham

1868 – 1957

James George Needham, for many years Professor of Entomology and Limnology at Cornell University, died July 24, 1957 in Ithaca, New York. Although his passing is deeply mourned by his friends and colleagues at Cornell, and around the world, we are thankful that a man of such unusual personal and professional stature could serve his profession and his fellow men for so long a period. He was in his 89th year. Although troubled in recent years by the common infirmities of later life, he was active well beyond the age of 85 and the great mind was fully alert to the end.

Born in Virginia, Illinois, on March 18, 1868, Dr. Needham was educated in the public schools there and at Knox College where he earned the B. S. and M. S. degrees. He became a teacher at Knox and during the late nineties wrote a text "Elementary Lessons in Zoology" which came to the attention of Professor Comstock at Cornell. Soon Comstock invited Needham to become a Goldwin Smith Scholar at Cornell and the two worked together on the morphology of wing venation in insects. The classic results of this endeavor are well known and will always be required reading for all students of entomology.

Dr. Needham was Professor of Biology at Lake Forest University from 1898 until 1907 when he returned to Cornell to teach Limnology, to become a world leader in this branch of biology, and to found a tradition of excellence in this field that still flourishes at Cornell. Soon after Dr. Needham's return to Cornell, Dean Liberty Hyde Bailey asked him to present a course in general biology designed for students who might otherwise have no contact with the field of biology. The course was highly successful and remains so today, attracting about 300 students each year from all colleges at Cornell.

Following the retirement of Professor Comstock in 1914, Dr. Needham was appointed Head of the Department of Entomology at Cornell and served in this capacity until his retirement in 1935. For Dr. Needham retirement was not a turning point but just a milestone in a great career. His research activities went on and papers continued to appear at regular intervals. A glance at his bibliography shows that over 150 of his approximately 350 publications appeared after retirement.

More careful study of the bibliography shows the unusual breadth of the man's interests, and his ability to deal with many diverse subjects in a thoroughly scholarly manner. While his greatest scientific works dealt with the taxonomy of aquatic insects, we find such titles as "The common ground of poet and naturalist," "The common ground of science and religion," "The world's moral outlook," and "About ourselves: A survey of human nature from the zoological viewpoint." His notable talent in the field of biographical writing is evident in his account of the lives of Professor and Mrs. Comstock that he titled "The lengthened shadow of a man and his wife."

One of the highest and most gratifying tributes that a college professor can receive is the respect and admiration of his graduate students, and this Dr. Needham enjoyed in full measure. Those of us who were present will always remember his appearance at a Cornell luncheon at our Richmond meetings a few years ago. Each of the more than 100 present was asked to introduce himself, identify the years spent at Cornell, and the Professor with whom he studied. By chance Dr. Needham was the last to rise, and his eyes were moist as he smiled and acknowledged the long, standing ovation that followed. No words were spoken. None were needed.

Sometimes a few paragraphs from a man's writings reveal more of his character, philosophy, and accomplishments than many pages of eulogy prepared by his contemporaries or his survivors. Dr. Needham's Christmas card for 1949 had on its cover a silhouette of an old pine tree, which still stands in the grounds of his home in Ithaca, and under it the simple inscription "Christmas 1949." Inside the folded card were the following short paragraphs that could have come only from the mind of a man in complete accord with nature:

"HERE IS A PICTURE OF MY LIFE—perhaps of yours too, my friend, to whom I send this photo silhouette. This old pine stands where I see it daily against the morning sky.

One day it seemed to say to me;
"How does the world use you?"
And I was moved to reply;
"Much as it uses you."

"For I saw that this tree and I had long been sojourners together on the earth; warmed by the same sun; fed from the same soil; taking the ups and downs of life that are the lot of all the living.

"I saw in that upstanding bole the sign of a sheltered youth, when it was a sapling like the young pines near it now, full of green branches. There below the crown, a little slant and two low stubs tell of careers that were entered upon and later abandoned. But the main fork above them led on upward into the two continuing interests of later years.

"That scragly crown tells of former days when it stood in the unbroken forest among competitors for light and standing room. Those stubs tell of trouble; enterprises that had to be abandoned; investments that failed. The elbows tell of partial successes; bafflements; points where forward progress was stopped and growth turned in new directions for light.

"But the old tree has its place in the sun. Its top is still green. Each little twig is crowned with clustering needles that glisten in the sunshine, impart their woodsy fragrance to the atmosphere, and their soft tremulous music to the passing breeze.

"Even so, shadow and sunshine, dealt by the impartial hand of Mother Nature, fall alike on trees and men."

H. H. SCHWARDT

William J. Gerhard

1873–1958

On December 13, 1958, William J. Gerhard, Curator Emeritus of Insects at the Chicago Natural History Museum, passed away—quickly and in the midst of an active life, as he would have wished—just 3 weeks before his 86th birthday. His sudden death from a heart attack deprived the Museum of its oldest and one of its most dedicated, honored and beloved staff members.

Mr. Gerhard assumed charge of the then newly created Division of Entomology on September 16, 1901. He saw it grow from a division consisting of an "old roll-top desk, two pencils, two pads of paper, a small wooden cabinet" and about 24,000 insects, to a well-equipped modern division—with collections totaling more than a million and a quarter specimens—that has taken its place among the principal centers of systematic entomology. Although he retired as Curator in 1950, following a coronary thrombosis, Mr. Gerhard remained active as Curator Emeritus. In spite of physical limitations, he was rarely absent from work.

His last 8 years were probably among the most personally satisfying in his entire career, for, relieved of administrative duties, he devoted almost full time to arranging the fruits of his life work, especially the Strecker Collection of butterflies and moths, and his personal collection of Hemiptera which he gave to the Museum. Few men have the opportunity, as he did, of seeing most of their life work so preserved and organized that they can see it integrated with the future. He was

JAMES GEORGE NEEDHAM
1868 — 1957

meticulous and thorough in his work and did not undertake more than he could complete.

Mr. Gerhard was well-known as an authority on the classification of the Hemiptera, though he never wrote a single original paper on them. As a matter of fact, he published few papers, but he assisted many of his colleagues in their studies. He was truly a "handmaiden of Science." The author of the only comprehensive manual on the Hemiptera of Eastern North America stated in his introduction: "The work in its present

WILLIAM J. GERHARD
1873–1958

form would not have been possible had it not been for W. J. Gerhard, of the Field Museum. . . ."

He at all times submerged his personal interests for the good of the Museum, and no task was too menial, trivial or onerous for him. He performed many that were unrelated to his field, including planning and installation of the Hall of Lower Invertebrates at a time when there was no Curator in charge.

He was uncomplicated, highly predictable. He had sharply defined concepts of right and wrong, respect for authority, courage to defend his stand, stubborn self-reliance to the end, a strong belief in hard work. He was scrupulous to a fault, modest, and self-effacing. In some of these attitudes he was perhaps extreme, but it is refreshing and instructive in this day to know men who regard integrity and principles as realities, not merely indefinable concepts.

He devoted much time to helping amateurs and students, as well as professionals, and gave a number of beginning students an opportunity to learn about insects in his division. "The boys" who owe him an eternal debt of gratitude are many, the writer among them. The most notable of these perhaps, is Dr. William Mann, former Director of the National Zoo. Mr. Gerhard's sympathy with beginners probably dates to the time (1895–98) when he got his own early training in entomology as a Jessup Student at the Academy of Natural Sciences in Philadelphia under the tutelage of Dr. Henry Skinner.

His advanced formal schooling consisted of evening courses at Temple College, as well as private instruction in Latin during the time he was a Jessup Student. He spent a year (1898–99) in Bolivia where he collected butterflies and moths for A. G. Weeks, whose collection is now at Harvard. The following year he was partner in a second-hand scientific book business. In 1901 he was recommended by Dr. Skinner for the position at Field Columbian Museum.

In recognition of his role in North American entomology, Mr. Gerhard was elected a Fellow of the Entomological Society of America, of which he was a charter member, and of the American Association for the Advancement of Science. He was elected a Contributor to the Museum in 1954, for the gift to the Museum of his collection and library. He was born near Reading, Pennsylvania, January 3, 1873. He is survived by four daughters, two sisters and a brother.

RUPERT L. WENZEL,
Chicago Natural History Museum

BOOK REVIEW

THE ECOLOGY OF INVASIONS BY ANIMALS AND PLANTS, by CHARLES S. ELTON. 181 pp. Illus., Maps, John Wiley and Sons, Inc., New York 16, 1958. $5.25.

In Elton's words this book "is about ecological explosions"—silent explosions characteristic of organisms suddenly relieved of the restraining forces of their environment. He believes that man is the cause and often the victim of one of the greatest convulsions in the history of the world's fauna and flora. Isolating barriers that marked the boundaries of Wallace's Realms have crumbled before man's conquest of the globe. Along with domestic animals and plants, a legion of camp-following and hitch-hiking organisms have accompanied him to every habitable land. Biotas that evolved in geographic and ecological isolation for at least 20,000,000 years have been disrupted and in some cases virtually displaced by alien animals and plants.

Within the bounds of their native homes, most organisms live unobtrusively in reasonably stable communities. Each animal and plant lives in a niche where it utilizes a portion of the total energy available to the community and normally relinquishes part of its share to parasites and predators that in turn give up energy to still another consumer level. In such a community, energy is transferred at a regulated steady rate analogous to the even flow of heat from a well banked and dampered stove. In case after case discussed by Elton, alien species have hungrily exploited energy resources at the expense of native biotas. In the absence of their natural enemies, they have increased without restraint, often exhausting their food resources and destroying the invaded community—just as the unbanked fire with an open draft quickly burns all its fuel, and perhaps the house as well.

The species he uses to illustrate the consequences of such invasions are mostly those having economic importance. They were selected not because of their importance, but because detailed information on their behavior is available, making it possible for him to map their distribution, and in some degree evaluate their impact on the invaded environments.

While the first seven chapters are directly concerned with the causes and effects of invasions, the last two deal with conservation. Elton recognizes that people must use land—for crops and the multitudinous purposes of modern human society. He agrees that conservation for pleasure, or instruction, or as some would allege, the rights of other animals, must not take precedence over human survival. Rather, he feels that man's survival depends upon his finding and applying some wise principle of co-existence with nature.

With this in mind Elton states his case for "conservation of variety". Certainly no ecologist will debate his point that communities richest in number of plant and animal species are the most stable and least likely to be disrupted by either native or naturalized pests. He regards variety as desirable both for practical and aesthetic reasons for in his words, hedgerows and weed patches not only provide valuable refuges but also "a great deal of visual pleasure to the traveler". 50 plates, 51 figs., 297 references and a seven page index add to the interest and usefulness of the book.

REECE I. SAILER,
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